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Saccharina latissima forest on very sheltered upper infralittoral rock

MarLIN – Marine Life Information Network
Marine Evidence-based Sensitivity Assessment (MarESA) Review

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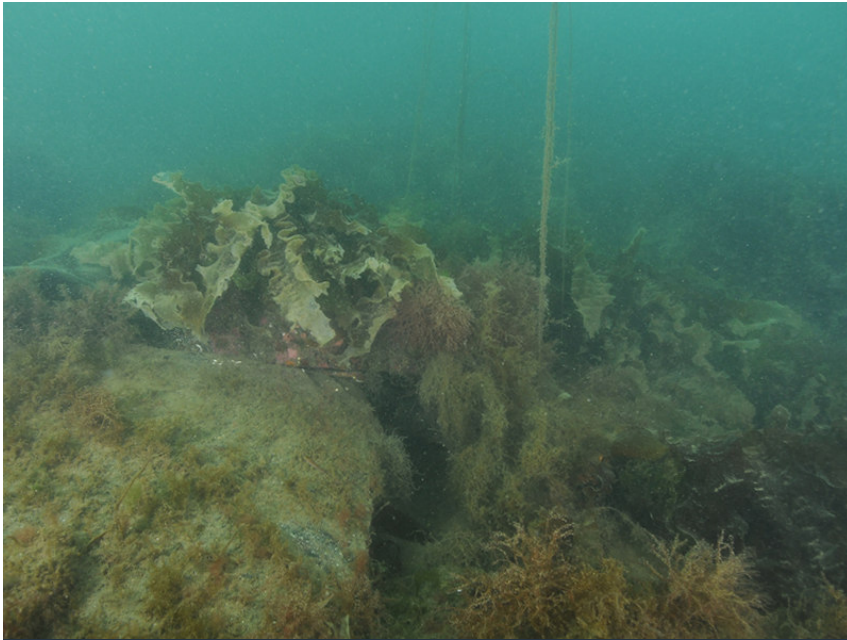
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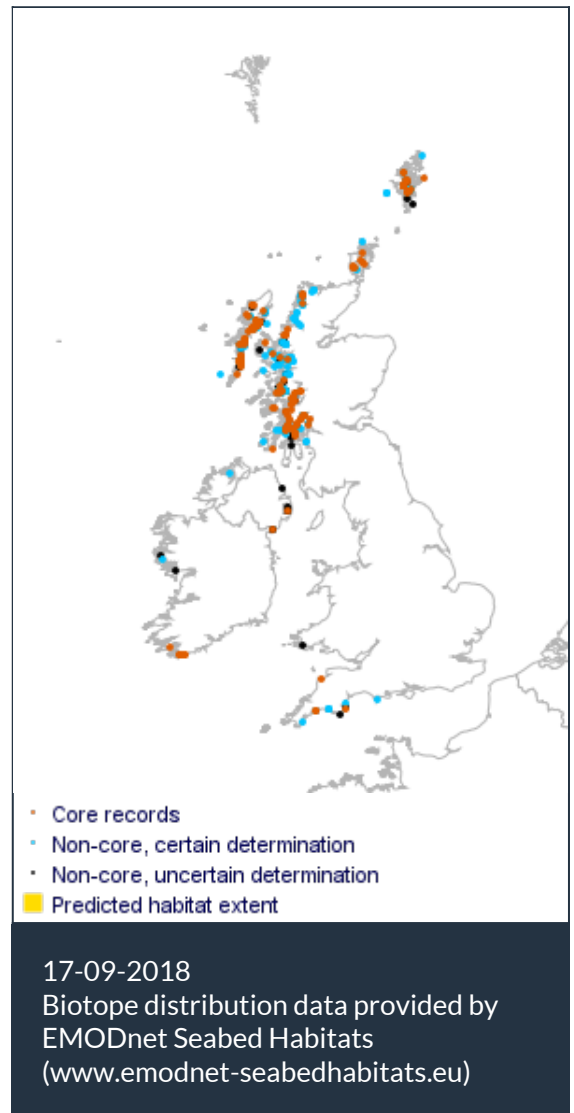


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Saccharina latissima on very sheltered infralittoral rock
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Researched by Claire Jasper Refereed by This information is not refereed.

Summary

UK and Ireland classification

EUNIS 2008	A3.3132	<i>Laminaria saccharina</i> forest on very sheltered upper infralittoral rock
JNCC 2015	IR.LIR.K.Slat.Ft	<i>Saccharina latissima</i> forest on very sheltered upper infralittoral rock
JNCC 2004	IR.LIR.K.Lsac.Ft	<i>Laminaria saccharina</i> forest on very sheltered upper infralittoral rock
1997 Biotope	IR.SIR.K.Lsac.Ft	<i>Laminaria saccharina</i> forest on very sheltered upper infralittoral rock

Description

Sheltered to extremely sheltered sublittoral fringe and infralittoral bedrock, boulders and cobbles characterized by a dense canopy of the kelp *Saccharina latissima*. In such sheltered conditions, a

distinct sublittoral fringe is not always apparent and this biotope can therefore extend from below the *Fucus serratus* zone (Fserr) into the upper infralittoral zone, though there may be a mixed *Saccharina latissima* and *Laminaria digitata* zone (Slat.Ldig) in between. There is a relatively low species diversity and species density due to a combination of heavy siltation of the habitat and the lack of light penetrating through the dense kelp canopy. Only a few species of red seaweeds are present compared with Slat.Ldig or LhypSlat. The most commonly occurring red seaweeds are *Delesseria sanguinea*, *Phycodrys rubens*, *Bonnemaisonia hamifera* and coralline crusts. Brown seaweeds are also sparse and generally comprise *Chorda filum* and ectocarpoids. At extremely sheltered sites, where there is a heavy silt cover on the rock and the kelp fronds, the sub-flora is reduced to a few specialised species able to tolerate these conditions, such as the cartilaginous seaweeds *Polyides rotunda* and *Chondrus crispus*. Ascidians such as *Clavelina lepadiformis*, *Ascidiella aspersa* and *Ascidia mentula* can remain prominent in such conditions, often occurring on steep or vertical rock which is subject to less siltation. The variety of red seaweeds is further reduced where grazers such as the urchin *Echinus esculentus* and the top shell *Gibbula cineraria* are present. The keelworm *Spirobranchus triqueter*, the crab *Carcinus maenas* and the hermit crab *Pagurus bernhardus* can be present. Geographical variations: Northern sites: in sheltered sealochs the most conspicuous fauna in these forests are the large solitary ascidians *Ciona intestinalis*, *Ascidiella* spp. and *Ascidiella mentula* which tend to occur in greater abundance than in the mixed kelp forests (LhypSlat). In common with mixed forests, echinoderms are consistently present in low abundance: the featherstar *Antedon bifida*, common starfish *Asterias rubens*, the brittlestar *Ophiothrix fragilis* and the urchin *Echinus esculentus* are typically present. Saddle oysters *Pododesmus patelliformis* and chitons *Tonicella marmorea* can occur in high abundance at some sites. The anthozoan *Anemonia viridis* is often more prevalent at the extremely sheltered sites. The communities of the sheltered voes and sounds of Shetland and Orkney are similar to those present in the mainland sealochs. Southern sites: sheltered infralittoral rock is not commonly found outside of the fjordic sealochs. In south-west Britain, where sublittoral rock does occur in shallow marine inlets, the waters are more turbid than in the sealochs, generally limiting kelp to the sublittoral fringe zone. Echinoderms are rare or absent from the south-western *Saccharina latissima* forests. A far greater diversity of red seaweeds is associated with the south-western sites: *Palmaria palmata*, *Gracilaria gracilis*, *Phyllophora pseudoceranoides*, *Cystoclonium purpureum*, *Rhodophyllis divaricata*, *Ceramium nodulosum* and *Polyneura bonnemaisonii* typically occur.

Although this biotope may occur below a mixed kelp canopy that occupies the sublittoral fringe (Slat.Ldig or Ldig.Ldig) at some sites it extends directly into the sublittoral fringe and abuts the *Fucus serratus* zone (Fserr or FserX on mixed substrata). Where suitable hard substrata are available, the *Saccharina latissima* diminishes in abundance (typically Frequent) with increasing depth to form kelp park (Slat.Pk). (Information from Connor *et al.*, 2004; JNCC, 2015).

↓ Depth range

Lower shore, 0-5 m

Additional information

As the available evidence, for most pressures, does not distinguish between IR.LIR.K.Slat.Ft and IR.LIR.K.Slat.Pk the information represent the sensitivity of both biotopes. Unless otherwise indicated all assessments are considered to apply to both biotopes.

✓ Listed By

- none -

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Sensitivity review

Sensitivity characteristics of the habitat and relevant characteristic species

This biotope is dominated by the opportunistic kelp *Saccharina latissima* and is characterized by high levels of siltation on bedrock, boulders and in some cases cobbles (Connor *et al.*, 2004). The density and diversity of associated organisms in this biotope is low as the combination of kelp canopy and siltation reduces light availability and increases scour. Robust foliose red algae and coralline crusts occur under the kelp canopy and ascidians are found within all *Saccharina latissima* biotopes, together with grazing urchins. In extremely sheltered high silt conditions (IR.LIR.K.Slat.Ft) the associated flora may be limited to a few specialist species of red cartilaginous seaweeds (e.g. *Polyides rotunda* and *Chondrus crispus*). In general, sites in south-west England have a higher diversity of red macroalgae than those of Scotland and Ireland. These biotopes are found in sheltered inlets, fjordic sealochs and loughs (south west England, Scotland and Ireland). For southwestern biotopes, echinoderms are rare or absent from *Saccharina latissima* forests resulting in a higher diversity of red seaweeds.

This biotope occurs in areas sheltered from wave action and strong water currents. As the kelp species, *Saccharina latissima* is the key characterizing species defining this biotope group, the sensitivity assessments are based largely on this species alone. *Saccharina latissima* is also the key habitat structuring species within this biotope and loss of this species would negatively affect the associated biological assemblage and result in the loss of this biotope. Although a range of species are associated with the biotope at low abundance, these species occur in a number of other rock biotopes and, therefore, do not specifically define this biotope group. Although these species contribute to the structure and function of the biotope they are not considered key species and are not specifically assessed.

As the available evidence, for most pressures, does not distinguish between IR.LIR.K.Slat.Ft and IR.LIR.K.Slat.Pk the information represents the sensitivity of both biotopes. Unless otherwise indicated all assessments are considered to apply to both biotopes.

Resilience and recovery rates of habitat

Saccharina latissima (studied as *Laminaria saccharina*) was the prominent kelp species on the concrete blocks (a minimum of 1.3 m in diameter) six months after removal of all vegetation (Kain, 1975). Without competition from other kelp species, *Saccharina latissima* populations increase their biomass within two years, while its density decreases (Mikhaylova, 1999). Re-attachment of dislodged *Saccharina latissima* may occur in certain conditions, with dislodged individuals growing new haperon (root-like structures) that subsequently attach to the substratum (Burrows, 1958). Unattached 'loose lying' populations of *Saccharina latissima* (studied as *Laminaria saccharina*) have been documented in Port Erin Bay, Isle of Man (Burrows, 1958). Indicating that apart from the earliest stages of sporophyte development, attachment to the substratum is not essential for growth. It is, therefore, possible that a few individuals could survive displacement, although this is not considered as a significant pathway for the biotope's recovery.

Saccharina latissima has a typical heteromorphic life history, in which a microscopic gametophyte alternates with a macroscopic adult, the sporophyte. The sporophyte's lifespan is normally two to four years, although older specimens have been recorded from a fjord in Greenland (Gayral & Cosson, 1973, Borum *et al.*, 2002). The growth of the lamina occurs from its base, potentially enhancing its resistance to grazing (Kain, 1979). Juvenile sporophytes take eight months to reach

an average size (1-2 m in length; Gerard, unpublished, cited in Gerard and Du Bois, 1988). Growth rates for sporophytes are greatest between 10-15°C, with tissue growth occurring from March to November (7 m depth, Bolton & Lüning, 1982, Nielsen *et al.*, 2014). Despite this, elongation of the frond only occurs between March and May due to high levels of abscission from July to November (Nielsen *et al.*, 2014). Temperature is a major factor affecting growth in *Saccharina latissima*, with decreased growth rates evidence above 16°C, and 50-70% growth reduction at 20°C (Bolton and Lüning, 1982).

Saccharina latissima's reproductive period is defined by the presence of sori (reproductive tissue) on its fronds. Sori are first produced by *Saccharina latissima* individuals of 4-5 months old and may occur for 1-9 concurrent months a year (studied as *Laminaria saccharina*, Parke 1948; Lüning 1979; Lee & Brinkhuis, 1988). This contrasts with other kelp species including *Laminaria digitata* and *Laminaria hyperborea* which reach maturity between 18-20 and 15 months respectively (Perez, 1971, Kain, 1975). Formation of sori (reproductive tissue) occurs at temperatures below 18°C (Bartsch *et al.*, 2013) from October to March/April (Andersen *et al.*, 2011). A minimum of 10 weeks a year between 5-18°C is needed for subsequent spore formation (Bartsch *et al.*, 2013). Thus temperature and season impact the level of reproductive activity. If environmental conditions for spore survival are not favourable, then the development of the gametophytes can be delayed for a short period, creating a level of resistance against short-term environmental changes (Van den Hoek *et al.*, 1995). Despite this ability, seaweeds, in general, are considered particularly vulnerable to short-term warming events (Dayton & Tegner, 1984; Smale & Wernberg, 2013; Wernberg *et al.*, 2013; from Smale *et al.*, 2013). Recruitment of *Saccharina latissima* generally occurs in the highest numbers from December to January (Andersen *et al.*, 2011).

Evidence on *Saccharina latissima*'s spore dispersal is limited. The passive dispersal of spores is reliant on local current and wave mediated water movements (Cie & Edwards, 2011). Kelp larval dispersal varies with location and species, *Macrocystis* spores in Australia may travel 1 km (Gaylord *et al.*, 2006), while the spores of *Laminaria digitata* have a dispersal range of 600 m (Chapman, 1981). In conditions of low water movement, typical of this biotope, larval dispersal range is likely to be depressed, with the majority of recruitment occurring within the biotope. The reforestation of historic kelp beds off Norway indicate that natural re-colonization was prevalent in the past (Moy and Christie, 2012). Andersen (2013) suggests that this, and other regional studies (see Andersen 2013 and the references herein) are illustrative of population connectivity and long distance dispersal in *Saccharina latissima*. *Saccharina latissima* exhibits a high degree of plasticity between populations with kelp from Maine, the USA able to withstand greater temperatures than their northern, New York counterparts (Gerard and Du Bois, 1988).

Interactions with other species may also alter the recovery of this biotope and in some instances, the interactions may be mediated by the effects of human activities. Grazers are responsible for less than 20% of kelp produced nutrients entering the food web; the majority enters as detritus or dissolved organic matter. Direct grazing of kelp is rare, with exceptions including the blue-rayed limpet (Krumhansl & Scheibling, 2012). However, in conditions of stress, grazers may change their feeding activity and directly graze the kelp. Laboratory choice experiments indicated that *Echinus esculentus* preferentially feeds on bryozoan encrusted *Saccharina latissima* over *Laminaria digitata*, meaning that the key species of this biotope may be more vulnerable to grazing than its counterparts (Bonsdorff & Vahl, 1982). Uncontrolled grazing of kelps by herbivores, including sea urchins, may result in detrimental consequences to the biotope. In Nova Scotia (Atlantic coast of Canada) a study on the kelp *Laminaria longicruris* and its understory of *Laminaria digitata* indicate that grazing sea urchins may have prevented the kelp biotope's regeneration after harvesting. Removal of the urchin's predators through direct harvesting (e.g. of fin fish) or indirect elimination

of the kelp canopy, leads to an urchin population increase which, unchecked by predation may result in the formation of barrens and the loss of the biotope (Bernstein *et al.* 1981; Estes & Duggins 1995; Ling *et al.*, 2009). Heavy biofouling has been indicated to cause premature death and decreased reproductive output in *Saccharina latissima* (Saier and Chapman, 2004, Andersen *et al.*, 2011). This indicates that a decrease in grazers which feed on these epibionts could be detrimental to the biotope's identity, especially in the light of future global sea temperature increases, which favour the growth of ephemeral algae (Andersen *et al.*, 2011).

Many of the Rhodophyta e.g. *Delesseria sanguinea*, are perennial species that may persist for several years. For instance, Dickinson (1963) suggested a lifespan of 5-6 years for *Delesseria sanguinea*. However, Kain (1984) estimated that 1 in 20 specimens of *Delesseria sanguinea* may attain 9 - 16 years of age. Kain (1975) examined recolonization of cleared concrete blocks in a subtidal kelp forest at Port Erin, Isle of Man. Red algae colonized blocks within 26 weeks in the shallow subtidal (0.8m) and 33 weeks at 4.4 m. *Delesseria sanguinea* was noted within 41 weeks (8 months) at 4.4 m in one group of blocks and within 56-59 days after block clearance in another group of blocks. This recolonization occurred during winter months following spore release and settlement, but not in subsequent samples (Kain, 1975). This suggests that colonization of *Delesseria sanguinea* in new areas is directly dependent on spore availability. Rhodophyceae have non-flagellate, and non-motile spores that stick on contact with the substratum. Norton (1992) noted that algal spore dispersal is probably determined by currents and turbulent deposition. However, red algae produce large numbers of spores that may settle close to the adult especially where currents are reduced by an algal turf or in kelp forests. However, in her recolonization experiments Kain (1975) while *Laminaria digitata* was considered re-established two years after removal, with the characterizing red foliose algae followed one year later, that is, took up to three years to reestablish prior abundance.

The community experiences constant levels of scour with periods of intense scour during winter storms so that the community is dominated by rapid colonizing opportunistic species that grow and mature rapidly, e.g. the ascidians, keel worms (*Spirobranchus* spp.) or mobile species such as the echinoderms. For example, any of the sessile fauna present in the biotope such as ascidians are considered to be dynamic and fast growing (Sebens, 1985). In clearance experiments, Sebens (1985, 1986) investigated recolonization of epifauna on vertical rock walls. He reported that rapid colonizers such as encrusting corallines, encrusting bryozoans, amphipods and tubeworms recolonized within 1-4 months. Ascidians such as *Dendrodoa carnea*, *Molgula manhattensis* and *Aplidium* spp. achieved significant cover in less than a year, and, together with *Halichondria panicea*, reached pre-clearance levels of cover after 2 years. Similarly, ascidians colonized an artificial reef in Poole Bay, England within a few months e.g. *Aplidium* spp. (Jensen *et al.*, 1994). *Clavelina lepadiformis* most likely has a short lifespan, of approximately 2 years. The larval phase is short, and metamorphosis into adults is rapid, so dispersal may be limited. Similarly, *Ciona intestinalis* has a short-lived ascidian tadpole larvae, although larvae may be produced on mucus strings so that dispersal is probably increased. Nevertheless, both species grow and mature quickly and can probably colonize areas quickly from local populations, for example *Ciona intestinalis* is a fouling species. Large mobile species such as sea urchins, starfish and crabs would migrate into the area rapidly.

Resilience Assessment. The rapid maturation of *Saccharina latissima* (4-5 months), when compared to other kelps means that this biotope should have a relatively fast recovery phase (less than two years) as indicated by its initial growth in areas cleared of other kelp species. The biotope is characteristic of areas subject to scour, especially during winter months and storms, so that the resident community is dominated by opportunistic and rapidly recruiting species. *Saccharina*

latissima species has been noted as one of the first algal species to recolonize disturbed substratum. The associated biota of *Saccharina latissima* are mainly substratum dwelling, their return to the biotope is likely to depend on the recovery of *Saccharina latissima* and is therefore likely to occur after the initial stages of recovery by *Saccharina latissima*. If removed completely red algae are likely to return within a year (Kain 1975) but do not reach the diversity and cover found at Port Erin, due to the inherent disturbance of this biotope due to scour. The density of these organisms is also dependent on the recovery of *Saccharina latissima* and therefore the recovery of the associated organisms is likely to lag behind the recovery of *Saccharina latissima*. The increase in biomass and decrease in stand density of *Saccharina latissima* within the first two years of re-growth in the White Sea suggests that the stand was stabilizing and may have reached near-maturity, again indicating a short recovery phase. Based on the opportunistic nature of *Saccharina latissima* and its ability to grow in conditions unfavourable to other kelp species, together with the opportunistic nature or mobility of the other members of the the community this biotope's resilience is regarded as 'High' (<2 years), even where removal is extensive (resistance is 'None'), provided there is an external source of zoospores, or larvae entering the location.

Hydrological Pressures

	Resistance	Resilience	Sensitivity
Temperature increase (local)	Medium	High	Low
	Q: High A: Medium C: Medium	Q: High A: High C: High	Q: High A: Medium C: Medium

Saccharina latissima is found in the NW Atlantic and North Pacific (Wilce 1965; Druehl, 1970; Lüning 1990), typically occurring between 40°N and 80°N. In Europe, *Saccharina latissima* occurs from Portugal to Spitsbergen (Van den Hoek & Donze, 1967, Lüning, 1990). Its distribution suggests a tolerance to a chronic temperature change (e.g. by 2°C for a year). Other associated organisms to this biotope may fair less well. Exposure to high short-term temperature increases are likely to result in stress, however, the recovery of this biotope is likely to be rapid. There is a general consensus in the literature that increases in temperature are likely to have a more detrimental effect than decreases in temperature (Andersen *et al.*, 2013, Nielsen *et al.*, 2014).

Temperature ecotypes have been suggested for *Saccharina latissima* populations near its southern limit off the USA coastline. Algae from New York, which experience water temperatures in excess of 20°C each summer, exhibit greater temperature tolerance than algae from Maine, where temperatures rarely exceed 17°C (Gerard & Du Bois, 1988). Three weeks of exposure to temperatures greater than 20°C in the field resulted in 50% mortality of algae from New York, while 100% of the algae from Maine died (Gerard & Du Bois, 1988). In comparison, individual *Saccharina latissima* from Helgoland in the southern North Sea undergo disintegration of blade tissue after 3 months at 15°C (Lüning, 1988).

The life cycle of kelps is considered sensitive to temperature. At temperatures greater than 15°C, higher photon flux densities are required to reach similar proportions of fertility to their counterparts kept at lower temperatures (Lüning, 1990), while photon fluence rates have been noted to rise concomitantly whilst photosynthetic efficiency decreases (Davison *et al.*, 1991). Sporogenesis in *Saccharina latissima* requires a minimum period of 4 weeks at or below 15°C combined with short day lengths in order to occur (Müller *et al.*, 2009). Germination of zoospores is also sensitive to temperature and may be population specific, with germination inhibited at 20°C in the laboratory, but exceeding 90% in field populations collected in July when photo fluence rates were 5 $\mu\text{E m}^{-2} \text{sec}^{-1}$ (Lee & Brinkhuis, 1988). The same study found that gametophyte growth

improved with increasing water temperatures between 4-17°C and that fecundity was greatest between 7-17°C.

Sporophyte growth has been recorded between 10-15°C with 50-70% reduction in growth at 20°C (Bolton & Lüning, 1982). For the gametophytes and young sporophytes of *Saccharina latissima*, the upper temperature tolerance is 22°C with exceptions including the growth of gametophytes in Long Island Sound at 23°C (Lee & Brinkhuis, 1988). A temperature of 23°C is also considered to be the maximum survival temperature for gametophytes from three European populations of *Saccharina latissima*, with disintegration occurring after 3 weeks (Bolton & Lüning, 1982). Although a more conservative estimate of *Saccharina latissima*'s upper temperature limit was considered by Lüning (1990) to be 20°C. In the summer of 1983 (the hottest on record before July 2009), bleaching of *Saccharina latissima* sporophytes was evident in Plymouth Sound and on the Isle of Man (Hawkins & Hartnoll, 1985). Research showed that growth reduction was evident at only 5°C above the optimum temperature range for *Saccharina latissima* (10-15°C) (Kain 1979; Bolton & Lüning 1982; Andersen *et al.*, 2013).

In an experiment observing gene expression in *Saccharina latissima*, a greater representation of genes associated with high temperature response than those for low temperatures was evident, suggesting that higher temperatures are more detrimental to *Saccharina latissima* (and therefore the biotope) than low temperatures (Heinrich *et al.*, 2012). A permanent change to the local temperature regime may result in a shift to ephemeral algae which then form a barrier to future settlement of *Saccharina latissima* slowing or stopping recovery of the biotope (Moy & Christie, 2012).

Increased temperatures bring with them increased growth of epiphytic ephemeral algae. Excessive growth on kelp by these species has been reported to result in high mortality rates within the kelp populations on the North American coast (Lee & Brinkhuis, 1988, Levin *et al.*, 2002, Scheibling & Gagnon, 2006). Krumhansl & Scheibling (2011) also found negative effects in growth in conjunction with increasing temperatures, however, they also highlighted the role which epiphytic loading enhances blade tissue loss (Andersen *et al.*, 2013). If environmental conditions for spore survival are not favourable, then the development of the gametophytes can be delayed for a short period, creating a level of resistance against short-term environmental changes (Van den Hoek *et al.*, 1995). Despite this ability, seaweeds, in general, are considered particularly vulnerable to short-term warming events (Dayton & Tegner, 1984; Smale & Wernberg, 2013; Wernberg *et al.*, 2013; from Smale *et al.*, 2013). Recruitment of *Saccharina latissima* generally occurs in the highest numbers from December to January (Andersen *et al.*, 2011).

The tolerance of red algae to temperature changes varies considerably and those of the littoral zone typically have a greater tolerance to both increased and decreased temperature, than those of the sublittoral (see Gessner, 1970,). Sublittoral red algal species, *Sphondylothamnion multifidum*, *Cryptopleura ramosa* and *Rhodophyllis divaricata* were capable of surviving at 27 °C, while other species such as *Callophyllis laciniata*, *Calliblepharis ciliata*, *Plocamium cartilagineum* and *Heterosiphonia plumosa* died within 12 hours in seawater at 27 °C. However, such a temperature increase exceeds that of the benchmark level. There is some evidence to suggest that blade growth in *Delesseria sanguinea* is delayed until ambient sea temperatures fall below 13°C, although blade growth is likely to be intrinsically linked to gametangia development (see Kain, 1987). *Delesseria sanguinea* is tolerant of 23°C for a week (Lüning, 1984) but dies rapidly at 25°C. The North Sea and Baltic specimens grew between 0-20°C, survived at 23°C but died at 25°C rapidly (Rietema, 1993). Rietema (1993) reported temperature differences in temperature tolerance between the North Sea and Baltic specimens. Lüning (1990) reports optimal growth in *Delesseria sanguinea* between 10

-15°C and optimal photosynthesis at 20°C. However, the upper limit of temperature tolerance is reduced by lowered salinity in Baltic specimens (Kinne, 1970; Kain & Norton, 1990). At low salinity, photosynthesis is restricted to a narrow range of temperatures in adult thalli whereas juvenile thalli have a wider response range (Lobban & Harrison, 1997; fig 6.27). It is likely therefore that within the subtidal an increase in temperature of 2°C in the long-term will have limited effect on survival, although it may affect initiation of new growth at the southern limits of the population. An increase of 5°C in the short-term may affect survival if the ambient temperature is increased above 23°C.

Bishop (1985) noted that gametogenesis of *Echinus esculentus* proceeded at temperatures between 11-19°C although continued exposure to 19°C destroyed synchronicity of gametogenesis between individuals. Embryos and larvae developed abnormally after up to 24 hr at 15°C (Tyler & Young, 1998). Bishop (1985) suggested that *Echinus esculentus* could not tolerate high temperatures for prolonged periods due to increased respiration rate and resultant metabolic stress.

Sensitivity assessment. Responses of this biotope to an increase in temperature are clearly population specific. Those at the extremes of the biotope's temperature range are likely to be more affected than those at the centre of their range. An increase of 5°C for one month may affect the fecundity of *Saccharina latissima* for that year depending on when the increase occurs because sporogenesis in *Saccharina latissima* requires a minimum period of 4 weeks at or below 15°C combined with short day lengths. An increase of 2°C is more likely to affect those at the extremes of the biotope's range, the plasticity of *Saccharina latissima* may allow for populations to adapt to the new conditions over time, however, this is uncertain. The red algae community may survive a long-term increase in 2°C but may suffer mortality from short-term change by 5°C, especially if the resultant temperature exceeded 27°C. Echinoderms most of the subtidal echinoderms are probably stenothermal and will avoid increases in temperature. Therefore, the resistance of this biotope to an increase in temperature is assessed as '**Medium**'. Resilience is likely to be '**High**' so that sensitivity is assessed as '**Low**'.

Temperature decrease (local)

High

Q: High A: High C: Medium

High

Q: High A: High C: High

Not sensitive

Q: High A: High C: Medium

Saccharina latissima is found in the NW Atlantic and North Pacific (Wilce 1965; Druehl, 1970; Lüning 1990), typically occurring between 40°N and 80°N. In Europe, *Saccharina latissima* occurs from Portugal to Spitsbergen (Van den Hoek & Donze, 1967, Lüning, 1990). Its distribution suggests that the species would tolerate a chronic temperature change (e.g. by 2°C for a year). Other associated organisms to this biotope may fair less well. The urchin *Psammechinus miliaris* was adversely affected by the 1962/63 winter, while the crinoid (rosy feather star) *Antedon bifida* may have been lost from the Menai Straits following winter 1947 (D.J. Crisp pers. comm. to K. Hiscock).

The life cycle of kelps, in particular, their spore production stage is considered to be sensitive to temperature. The gametophytes of *Saccharina latissima* reportedly suppress growth below 10°C (Lüning, 1990). In a laboratory experiment with an Arctic population of *Saccharina latissima*, embryos achieved 100% germination at 0°C, but expressed lower rates of primary cell growth in comparison to those grown at 10°C. These lower rates of growth do not seem to impede the kelp's ability to compete successfully, with the species occurring in year round temperatures lower than 0°C in a high-arctic Fjord, Greenland (Borum *et al.*, 2002). Sjøtun & Schoschina (2002) cultivated *Saccharina latissima* from embryospores at 0°C in the laboratory and showed that oogonia were

produced 18-20 days after sporulation in comparison to a minimum of 20-24 days for *Laminaria hyperborea*, and 34 days for *Laminaria digitata*.

Under laboratory conditions chronic exposure to 5°C, after being maintained at 15°C, resulted in the adult sporophytes stage requiring a higher photon fluence rate to maintain net and light-saturated photosynthesis (studied as *Laminaria saccharina*, Davison *et al.*, 1991). This response is short-term, with the acclimation of growth temperatures over time buffering the depression in compensation point and light-saturated photosynthesis, allowing the alga to achieve similar rates of light-limited photosynthesis at both 5 and 15°C (Davison *et al.*, 1991). At 2°C, *Saccharina latissima* up-regulates the production of amino acids associated with Glutathione, an antioxidant, suggesting that below 2°C lowered growth rates are related to an increased energy expenditure on decreasing the effects of photo-oxidative stress (Heinrich *et al.*, 2012).

Cold damage usually changes the colour of red algae to a bright yellow orange. *Sphondylothamnion multifidum*, *Cryptopleura ramosa* and *Rhodophyllis divaricata* were partially or completely killed at 5°C. *Callophyllis laciniata*, *Calliblepharis ciliata*, *Plocamium cartilagineum* and *Heterosiphonia plumosa* survived -2 °C. *Delesseria sanguinea* and *Phycodrys rubens* succumbed at temperatures of -3 °C to -5 °C. During experimental attempts to adapt red algae to cold by maintaining them at -1 °C to + 1 °C for several months, a drop in the lethal temperature tolerance of *Delesseria sanguinea* and a few other species was detected, in the order of 1 to 2°C (Gessner, 1970). However, it is unlikely that seawater temperatures would fall below 0°C in the UK.

Sensitivity assessment. A decrease in temperature at the benchmark is not likely to impact biotopes at the centre of their temperature tolerances, however, those at its temperature limit are likely to experience decreases in abundance of *Saccharina latissima* (due to reduced reproduction and growth) if the temperature is lowered to 2°C for one year. If decreases of 5°C for one month occur, then the time of the year is vital in determining the response of this biotope as it may impact the fecundity of the *Saccharina latissima* population and growth of red algae. However, if the decrease is chronic the biotope should persist and is therefore considered to have a resistance of 'High' to this biotope. A resilience of 'High' is therefore also recorded, while the overall sensitivity of the biotope is 'Not sensitive', although, beyond the benchmark, the loss of the biotope may occur.

Salinity increase (local)

Medium

Q: High A: Low C: Low

High

Q: High A: High C: High

Low

Q: Medium A: Low C: Low

Both IR.LIR.K.Slat.Ft and IR.LIR.K.Slat.Pk are recorded from full salinity conditions but *Saccharina latissima* is also typical of variable or reduced salinity conditions (Connor *et al.*, 2004). In a laboratory experiment, *Saccharina latissima* (studied as *Laminaria saccharina*) survived successfully between 17-32 psu (Druehl, 1967). However, Gerard & Du Bois (1988) reported that *Saccharina latissima* had a salinity tolerance of 23-31 psu. Karsten (2007) tested the photosynthetic ability of *Saccharina latissima* under acute 2 and 5 day exposure to salinity treatments ranging from 5-60 psu. A control experiment was also carried at 34 psu. *Saccharina latissima* showed high photosynthetic ability at >80% of the control levels between 25-55 psu. Decreases in salinity to 5 psu for *Saccharina latissima* from Arctic Kongsfjorden (Spitsbergen) induced bleaching, indicative of cell damage after 5 days of incubation in the laboratory, while treatments decreasing from 20-10psu were associated with decreasing photosynthetic performance (Karsen, 2007). However, Birkett *et al.* (1998b) suggested that kelps are stenohaline and therefore long-term increases in salinity may be detrimental.

Optimum growth rates in algae cultured from UK waters were achieved at 31 psu, while 16 psu dramatically decreased growth rates and 8 psu resulted in the death of the alga (Burrows & Pybus 1971). In contrast, *Saccharina latissima* from the White Sea responded with decreased photosynthetic rates at 6-8 psu, while severe growth reductions were noted at 2 psu (Drobyshev, 1971). Juvenile sporophytes of *Saccharina latissima* can survive salinities of 13 for 3 weeks, however, at 10 psu the juveniles become severely stressed and the majority die (Spurkland & Iken, 2011a). In Arctic kelp, decreases in *Saccharina latissima* growth were associated with decreasing salinity (Spurkland & Iken 2011a). Neilsen *et al.* (2014) also associated low growth, with decreases in salinity in a field experiment in Danish waters; while Weile (1996), recorded low growths (5.4 mm/day) in areas < 14 psu. Responses of *Saccharina latissima* to salinity changes are population specific. Exposure to salinities outside a kelp's tolerance range causes osmotic and ionic stress (Kirst 1990) resulting in decreased efficiency of their photosynthetic apparatus (<20-25%, Kirst & Wiencke, 1995).

The associated biota are relatively tolerant to this changes in salinity, *Delesseria sanguinea* tolerates salinities of 11 psu in the North Sea, while the brittle star *Ophiothrix fragilis* occurs at salinities of 10-16 psu (Wolff, 1968). Associated echinoderms are likely to fair less well as they don't possess an osmoregulatory organ (Boolootian, 1966). At low salinities, urchins gain weight, and the epidermis loses its pigment; prolonged exposure is fatal. The coelomic fluid of *Echinus esculentus* is isotonic with seawater (Stickle & Diehl 1987). Because of this, a decrease in salinity within the benchmark may result in lowering the grazing pressure on the biotope and, may in the short-term be beneficial to the biotope.

Sensitivity assessment. At the benchmark, an increase in salinity from 'full' to 'hypersaline' (>40 psu) conditions for a year is unlikely to adversely affect *Saccharina latissima* population up to ca 55 psu (Karsten, 2007). Little evidence for the effects of hypersaline conditions on the associated flora and fauna was found, although most echinoderms are generally regarded as stenohaline (Russell, 2013). Therefore, the resistance is probably '**Medium**' to represent the potential loss of members of the associated flora and fauna. Resilience is probably '**High**' so that sensitivity is assessed as '**Low**'.

Salinity decrease (local)

High

Q: High A: High C: Medium

High

Q: High A: High C: High

Not sensitive

Q: High A: High C: Medium

Both IR.LIR.K.Slat.Ft and IR.LIR.K.Slat.Pk are recorded from full salinity conditions but *Saccharina latissima* is also typical of variable or reduced salinity conditions (Connor *et al.*, 2004). In a laboratory experiment, *Saccharina latissima* (studied as *Laminaria saccharina*) survived successfully between 17-32 psu (Druehl, 1967). However, Gerard & DuBois (1988) reported that *Saccharina latissima* had a salinity tolerance of 23-31 psu. Optimum growth rates in algae cultured from UK waters were achieved at 31 psu, while 16 psu dramatically decreased growth rates and 8 psu resulted in the death of the alga (Burrows & Pybus 1971). In contrast, *Saccharina latissima* from the White Sea responded with decreased photosynthetic rates at 6-8 psu, while severe growth reductions were noted at 2 psu (Drobyshev, 1971). Decreases in salinity to 5 psu for *Saccharina latissima* from Arctic Kongsfjorden (Spitsbergen) induced bleaching, indicative of cell damage after 5 days of incubation in the laboratory, while treatments decreasing from 20-10psu were associated with decreasing photosynthetic performance (Karsen, 2007). Juvenile sporophytes of *Saccharina latissima* can survive salinities of 13 for 3 weeks, however, at 10 psu the juveniles become severely stressed and the majority die (Spurkland & Iken, 2011a). In Arctic kelp, decreases in *Saccharina latissima* growth were associated with decreasing salinity (Spurkland & Iken 2011a).

Neilsen *et al.*, (2014) also associated low growth, with decreases in salinity in a field experiment in Danish waters; while Weile (1996), recorded low growths (5.4 mm/day) in areas <14 psu. Responses of *Saccharina latissima* to salinity changes are population specific. Exposure to salinities outside a kelp's tolerance range causes osmotic and ionic stress (Kirst 1990) resulting in decreased efficiency of their photosynthetic apparatus (<20-25%, Kirst & Wiencke, 1995).

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Sensitivity assessment. At the benchmark, a decrease in salinity from 'full' to 'reduced' (18-30 psu) for a year is unlikely to adversely affect *Saccharina latissima* population, although its abundance may decrease slightly if growth rates are impaired. However, if the changes were prolonged the associated flora and fauna may change, reflecting an increase in red algae and ascidians tolerant of reduced salinity, so that the biotope may come to resemble IR.LIR.KVS.SlatPhyVS or IR.LIR.KVS.SlatPsaVS. At the benchmark level, IR.LIR.K.Slat.Ft and IR.LIR.K.Slat.P are considered to have '**High**' resilience to the pressure. The biotope is considered to have '**High**' resilience and hence '**Not sensitive**' at the benchmark level.

Water flow (tidal current) changes (local)

High

Q: High A: Medium C: Medium

High

Q: High A: High C: High

Not sensitive

Q: High A: Medium C: Medium

The key characterizing species of this biotope, *Saccharina latissima* is unlikely to be directly affected by this pressure at the prescribed benchmark. Increased competition from other species (such as *Laminaria digitata* and *Laminaria hyperborea*) with the change in environmental conditions will pose an indirect threat, as this biotope is defined by low levels of water movement, and *Saccharina latissima* thrives best in these conditions. Tidal streams of >0.5 m/s or lower as described by Connor *et al.* (2004).

Comparisons between biomass yields (dry weight) from two sites found significantly higher yields of *Saccharina latissima* at the moderately exposed site over the sheltered site, with light exposure and water velocity cited as the determining factors of both populations health (Peteiro & Freire, 2013). The turbulence created by friction at the frond-water interface acts as a transport mechanism for nutrients from the water column to the algae and is called the boundary layer. In conditions which lack water motion, the transportation of dissolved gases and nutrients within the boundary layer may be significantly reduced, leading to diminished growth (Wheeler, 1980, Parker, 1981, 1982); although conditions of no water motion are rare in the field (Gerard, 1982). Water activity (wave, tidal and current mediated) may also be important for reducing sedimentation and the growth of filamentous algae which may compete with the key species in this biotope (Norton, 1978; Pihl *et al.*, 1994; Isæus, 2004; Moy *et al.*, 2006) and are the suggested reason for the absence of this biotope from extremely sheltered Norwegian waters (Bekkby & Moy, 2011). Despite this, populations of loose lying *Saccharina latissima* have been identified in areas of low water motion, in these conditions, attachment to the substratum does not appear to be important (Burrows, 1958); however if a lack of water movement results in a change in the

kelp's life history traits, this along with the likely change in associated species would be considered as equivalent to the loss of the biotope.

Saccharina latissima is absent from extremely sheltered conditions with little water flow in Norway. This infers that *Saccharina latissima* needs a minimum amount of water movement in order to survive; perhaps because of decreased competition from filamentous algae and sedimentation, but also because water flow maintains a nutrient flux and enhances light penetration to juvenile sporophytes by moving the fronds (Norton, 1978; Pihl *et al.*, 1995; Lobban & Harrison, 1994; Hurd, 2000; Isæus, 2004; Moy *et al.*, 2006; Bekkby & Moy, 2011). Decreased wave exposure also causes localised stagnation and de-oxygenation of the water column which would decrease survivorship in the area.

Saccharina latissima's morphology was noted to differ between a moderately exposed and sheltered site, with those at the moderately exposed site exhibiting a large surface area than those at the sheltered site (Peteiro & Freire, 2013). Kelps typically have a plastic morphology, in controlled laboratory experiments juvenile *Saccharina latissima* (studied as *Laminaria saccharina*) altered their morphology under different water flow exposures; mechanical longitudinal stress resulted in narrower blades of increased cell elongation, while a lack of tension leads to greater blade widths after 6 weeks (Gerard, 1987). This plasticity is likely to protect thallus damage in areas of greater exposure or in stormier conditions. Stronger water currents may dislodge the kelp from bedrock or cause damage by moving boulders and cobbles.

Larval dispersal is in part governed by the local hydrodynamic regime; increased turbulence is associated with an increase in biotope connectivity and therefore a loss of larvae from the local system. A decrease in wave and current mediated water flow is identified by lower connectivity with other sites and a higher settlement rate within the local biotope (Robins *et al.*, 2013). Therefore, an increase in water flow could result in larval loss from the local biotope, which if not balanced by a larval influx from another geographically different population, could result in the demise of the local biotope's health; with a shift in the age structure of the population and a death of young alga.

Red algae are found in a range of water flow regimes, e.g. *Delessaria sanguinea* is recorded from moderately strong to weak tidal flows. The ascidians are equally found in a range of tidal flow, and good water flow is considered important for suspension feeders, depending on species. However, *Clavelina lepadiformis* thrives in areas where there is very little, if any, water movement (for instance, Abereiddy Quarry, Pembrokeshire (Hiscock & Hoare, 1975) and *Ciona intestinalis* is remarkably tolerant of low flow rates and is frequently found in areas with minimal water exchange and renewal such as harbours, marinas and docks.

Sensitivity assessment. Water movement is a key defining feature of this biotope as *Saccharina latissima* is characteristic of sheltered, low energy habitats. However, it also occurs in strong water flow where scour (e.g. from mobile coarse sediment) and/or turbidity exclude other less opportunistic kelp species (e.g. *Laminaria digitata*). Therefore, while mobile sediments (e.g. cobbles) and siltation remain, an increase in water flow of 0.1-0.2 m/s may not have a significant effect on the biotope. Therefore, a '**High**' resistance and by default a '**High**' resilience to this pressure is recorded at the benchmark level. Hence, this biotope is regarded as '**Not sensitive**'.

Emergence regime changes

None

Q: Medium A: Low C: Medium

High

Q: High A: High C: High

Medium

Q: Medium A: Low C: Medium

The IR.LIR.K.Slat.Ft biotope is predominantly infralittoral while IR.LIR.K.Slat.Pk occurs below 5 m. Therefore, a change in emergence is unlikely to be relevant to IR.LIR.K.Slat.Pk. *Saccharina latissima* can withstand a degree of desiccation, many of the subordinate species, especially solitary sea squirts, are unlikely to survive an increase in emergence. Mobile species including sea urchins, brittle stars and feather stars are expected to move out of the biotope to deeper waters. The associated red macroalgae of this biotope will have species specific responses to both increases and decreases in emergence with those of a saccate morphology generally more resistant to increased emergence than their counterparts (Oates, 1985, 1986).

Air exposure causes desiccation, which prevents photosynthesis, thereby decreasing growth rates in *Saccharina latissima* (studied as *Laminaria saccharina*, Kain, 1979). Kelps are generally less tolerant to desiccation than other brown macroalgae (e.g. fucoids) and are therefore likely to be competitively out-competed at their upper limits (Davison & Pearson, 1996, Harker *et al.*, 1999). An increase in emergence would lead to a depression in the upper limit of the species distribution; the biotope's lower limits may extend down the shore as irradiance levels increase in areas previously too deep for light-saturated photosynthesis to occur. In conditions of low summer temperatures, *Saccharina latissima* has been documented as occurring in sheltered bays of the inner Porsangerfjord, North Norway, where the stands are completely drained at low tide (Sivertsen & Bjorge, 2015), suggesting that unique exceptions do exist in relation to this pressure, but are not the norm.

Sensitivity Assessment. This pressure is a key driver of biotope extent because emergence and local light regime define the limits of *Saccharina latissima*. In the case of a sea level rise, the change in light regime is suggested to cause the shifting of the biotope up the shore spatially, remaining within the environmental conditions of the sublittoral zone. If an obstacle to movement perpendicular to the shoreline (e.g. sea defence) is then combined with a change in the emergence regime this biotope could undergo compression of its range, a change from IR.LIR.K.Slat.Ft to IR.LIR.K.Slat.Pk (due to the increase in relative water depth), or may result in its local extinction. In the direct footprint of the impact resistance is, therefore 'None' (loss of >75%). Resilience is suggested as 'High' as the biotope is likely to develop in lower on the shore, under conditions of increased emergence and increased sea levels. The IR.LIR.K.Slat.Ft biotope is therefore considered to have 'Medium' sensitivity to the pressure.

Wave exposure changes (local)

High

Q: High A: Medium C: Medium

High

Q: High A: High C: High

Not sensitive

Q: High A: Medium C: Medium

IR.LIR.K.Slat.Ft was recorded from very wave sheltered to extremely sheltered conditions, while IR.LIR.K.Slat.Pk was recorded from sheltered to very sheltered condition (Connor *et al.*, 2004). The occurrence of *Saccharina latissima* and, therefore, this biotope can be predicted by the level of wave action experienced by a location (Bekkby & Moy, 2011). *Saccharina latissima* rarely grows in wave exposed conditions, as it is vulnerable to dislodgement from wave action and additionally may be attached to cobbles and boulders typical of this biotope, which may be overturned in conditions of increased wave action. Increased wave exposure is also likely to detrimentally affect deposit feeders and species inhabiting the sediment which typically overlays the substratum in this biotope.

In conditions of increased wave action, *Saccharina latissima* may gradually change position, shifting into the lower eulittoral (Birkett *et al.*, 1998b). Competition from other species such as *Laminaria digitata*, able to withstand higher levels of wave action, may out-compete *Saccharina latissima* under

natural conditions. *Saccharina latissima* has been cultivated in the presence of 6.4 m high waves (Buck & Buchholz, 2005), indicating that this competition is the likely driver of *Saccharina latissima*'s absence from exposed shores. In conditions of greater wave action, *Saccharina latissima* productivity (studied as *Laminaria saccharina*) was less than that of a sheltered population; this may have been due to greater nutrient availability in the sheltered site from a current of 0.5 meters/second/second (Gerard & Mann, 1979). Urchins have been noted to migrate out of kelp biotopes during storms and periods of high wave action, it is suggested that this is done to avoid damage by algal whiplash, which increases in turbulent conditions, temporarily decreasing the grazing pressures on the biotope (Lauzon-Gauy, 2007). When considered in conjunction with emergence, wave exposure is beneficial to *Saccharina latissima*, with wave spray acting to hydrate individual alga which would otherwise suffer from desiccation and decreased growth rates (Kain, 1979).

While *Saccharina latissima* is generally absent from wave-swept shores, it is also absent from extremely sheltered conditions in Norway. Inferring that *Saccharina latissima*'s needs a minimum amount of water movement in order to survive; perhaps because of decreased competition from filamentous algae and sedimentation, but also because wave action maintains a nutrient flux and enhance light penetration to juvenile and smaller sporophytes by moving the fronds (Norton, 1978, Pihl *et al.*, 1995, Lobban & Harrison, 1994, Hurd, 2000, Isæus, 2004, Moy *et al.*, 2006 Bekkby & Moy, 2011). Decreasing wave exposure also causes localised stagnation and de-oxygenation of the water column which would decrease survivorship in the area.

Sheltered conditions favour the growth of epiphytes, which decrease *Saccharina latissima*'s ability to withstand storm events and increased wave action, potentially increasing the vulnerability of this biotope to the pressure. The growth of the epiphytic bryozoan, *Membranipora membranacea* reduces the ability of individual alga to withstand wave action, increasing frond breakages by making them brittle and reducing the maximum stress, toughness and extensibility of the kelp blade materials (Krumhansl *et al.*, 2011). Andersen *et al.* (2011) suggested that in conditions of increased wave activity, water movement may act to clear the fronds' surface of epibiota, thus improving the health of the population in comparison to those in deeper and more wave sheltered areas.

The structure of kelp enables them to survive a range of wave conditions (Harder *et al.*, 2006). Comparisons between biomass yields from two sites found significantly higher yields at the moderately exposed site over the sheltered site, with light exposure and water velocity cited as the determining factors of both populations health (Peteiro & Freire, 2013). The blades of *Saccharina latissima* at the moderately exposed site were also found to have a large surface area than those at the sheltered site. Kelps typically have a plastic morphology, controlled laboratory experiments indicating that juvenile *Saccharina latissima* (studied as *Laminaria saccharina*) individuals alter their morphology under exposure to different water flow conditions, with mechanical longitudinal stress resulting in narrower blades of increased cell elongation while a lack of tension lead to greater blade width after 6 weeks (Gerard, 1987). This plasticity is likely to protect thallus damage in areas of greater exposure or in stormier conditions, although stronger water currents may dislodge the kelp from bedrock or cause damage by moving boulders and cobbles.

Sensitivity assessment. The plastic nature of *Saccharina latissima*'s structure means that it can withstand an increase in wave exposure. However, it may not be able to out-compete other species including *Laminaria digitata* in more wave exposed conditions, so that the biotope is likely to change, to either mixed kelp biotopes or biotopes dominated by *Laminaria digitata* in shallow

examples or *Laminaria hyperborea* in more exposed examples, so that the biotope will be lost. Nevertheless, a change in significant wave height of 3-5% is unlikely to have a significant effect on the biotope. Hence a resistance of '**High**' is recorded, with a resilience of '**High**', and the biotope is assessed as '**Not sensitive**' at the benchmark level.

Chemical Pressures

	Resistance	Resilience	Sensitivity
Transition elements & organo-metal contamination	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR

This pressure is **Not assessed** but evidence is presented where available.

Hydrocarbon & PAH contamination	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR
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This pressure is **Not assessed** but evidence is presented where available.

Synthetic compound contamination	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR
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This pressure is **Not assessed** but evidence is presented where available.

Radionuclide contamination	No evidence (NEv) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR
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No evidence

Introduction of other substances	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR
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This pressure is **Not assessed**.

De-oxygenation	High Q: Low A: NR C: NR	High Q: High A: High C: High	Not sensitive Q: Low A: Low C: Low
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No direct evidence on the effects of deoxygenation for *Saccharina latissima* was found in the literature, but reduced oxygen concentrations have been shown to inhibit both photosynthesis and respiration in macroalgae (Kinne, 1977). Despite this, macroalgae are thought to buffer the environmental conditions of low oxygen, thereby acting as a refuge for organisms in oxygen depleted regions, especially if the oxygen depletion is short-term (Frieder *et al.*, 2012). A rapid recovery from a state of low oxygen is expected if the environmental conditions are transient. In addition, this biotope occurs in areas of low water movement, implying that a degree of hypoxia may be inherent in the system. If levels do drop below 4 mg/l, negative effects on these organisms can be expected with adverse effects occurring below 2mg/l (Cole *et al.*, 1999).

Grazing of this biotope may be reduced as deoxygenation above the benchmark (anoxia) has been recorded as inducing the death for fish and invertebrates, including *Echinus esculentus* as a result of a *Gyrodinium aureolum* phytoplankton bloom in Mounts Bay, Penzance in 1978 (Griffiths *et al.*, 1979).

Sensitivity Assessment. Reduced oxygen levels are likely to inhibit photosynthesis and respiration but not cause a loss of the macroalgae population directly. However, small invertebrate epifauna may be lost, causing a reduction in species richness. As the biotope is not considered dependent in any way upon these species and as these are not considered key characterizing species this loss is not considered in the sensitivity assessment. Therefore, based on *Saccharina latissima* a resistance of 'High' is recorded. Hence resilience is likely to be 'High', and the biotope is probably 'Not sensitive' at the benchmark level.

Nutrient enrichment

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not sensitive

Q: NR A: NR C: NR

As a macroalgae, *Saccharina latissima* uptakes nitrogen and carbon from the water column in order to survive and grow. The nitrogen and carbon content of *Saccharina latissima* varies annually, in conjunction with growth periods and nitrogen availability (Nielsen *et al.*, 2014). Carbon is used for winter growth and is stored during the summer as carbohydrate, while nitrogen is used for summer growth, and is a limiting factor (Nielsen *et al.*, 2014). High ambient levels of phosphate and nitrogen enhance spore formation in *Saccharina latissima* (Nimura *et al.*, 2002), but will eventually inhibit spore production, particularly at the extremes of the alga's temperature tolerance (studied as *Laminaria saccharina*; Yarish *et al.*, 1990). *Saccharina latissima* from the east coast of Scotland, showed increased growth rates in the laboratory when nutrient levels were enhanced by 25% (Conolly & Drew, 1985). Enhancement of coastal nutrients is likely to favour those species with more rapid growth rates including turf forming algae (Gorgula & Connell, 2004). Epiphytic abundance and biomass on *Laminaria longicruris*, for example, increased under a eutrophic regime (Scheibling *et al.*, 1999) and resulted in a shift from kelp dominated biotopes to an ephemeral algae dominated biotope in Norway (Moy & Christie, 2012).

Sensitivity Assessment. The benchmark of this pressure (compliance with WFD 'good' status) allows for a slightly less diverse community of red, green and brown seaweeds with the greatest reduction in red species and an increase in the proportion of short-lived species under the WFD criteria for good status. The algae diversity in this biotope is already low with those remaining resistant to shading by kelp fronds and siltation. A further reduction in algal diversity would alter the biotope but would not result in loss of the biotope. However, the biotope is considered 'Not sensitive' at the pressure benchmark that assumes compliance with good status as defined by the WFD.

Organic enrichment

High

Q: High A: Medium C: Medium

High

Q: High A: High C: High

Not sensitive

Q: High A: Medium C: Medium

As a macroalgae, *Saccharina latissima* uptakes nitrogen and carbon from the water column in order to survive and grow. The nitrogen and carbon content of *Saccharina latissima* varies annually, in conjunction with growth periods and nitrogen availability (Nielsen *et al.*, 2014). Carbon is used for winter growth and is stored during the summer as carbohydrate, while nitrogen is used for summer growth (Nielsen *et al.*, 2014).

The amount of organic nitrogen a *Saccharina latissima* stand may be able to uptake varies with location; with *Saccharina latissima*'s nitrogen uptake by a fish farm in Tristein, Central Norway estimated as 1.2 t of nitrogen per hectare of kelp over one growth season (Wang *et al.*, 2014), while a similar setup in north-western Scotland predicted the removal of 5% waste nitrogen from 500 tonnes salmon over 2 years (Sanderson *et al.*, 2012). The excrement and unused feed for fish farms increased the levels of organic matter in their local vicinity. Evidence from the experimental culture of *Saccharina latissima* around fish farms showed enhanced growth rates by up to 61% at certain times in the year (Sanderson *et al.*, 2012). The quality of the nutrient source is also important with depressed growth rates associated with *Saccharina latissima* growing near a sewage sludge dumping ground in Liverpool Bay, Irish Sea (Burrows, 1971).

Sea urchins may survive on barren grounds near sewage outfall, anecdotally surviving on dissolved organic material, detritus, plankton and microalgae for prolonged periods (13 years). However the lifespan of the sea urchins in these conditions are severely depressed (Lawrence, 1975). This species may be more resistant to the pressure than *Saccharina latissima* and may overgraze the biotope, resulting in the loss of the biotope.

Sensitivity assessment. At the benchmark level (a deposit of 100 gC/m²/yr) this biotope should be resistant to the pressure, as suggested by the survival and enhanced growth of *Saccharina latissima* near fish farms where there were high levels of organic matter deposited. Resistance to this pressure is therefore regarded as '**High**', although beyond the benchmark, negative consequences of enhanced organic enrichment are possible. Resilience is therefore also regarded as '**High**' and the biotope is therefore probably '**Not sensitive**' at the pressure benchmark.

A Physical Pressures

	Resistance	Resilience	Sensitivity
Physical loss (to land or freshwater habitat)	None Q: High A: High C: High	Very Low Q: High A: High C: High	High Q: High A: High C: High

All marine habitats and benthic species are considered to have a resistance of '**None**' to this pressure and to be unable to recover from a permanent loss of habitat (resilience is '**Very low**'). Sensitivity within the direct spatial footprint of this pressure is, therefore '**High**'. Although no specific evidence is described confidence in this assessment is 'High', due to the incontrovertible nature of this pressure.

	Resistance	Resilience	Sensitivity
Physical change (to another seabed type)	None Q: High A: High C: High	Very Low Q: High A: High C: High	High Q: High A: High C: High

A change in substratum type from bedrock to sediment would render the habitat unsuitable because kelp requires a stable substratum on which to settle. No evidence of this biotope occurring on sedimentary substratum was found in the literature. This biotope is anecdotally scarce on the south-east coast of Ireland, in particular, Counties Wicklow and Wexford, due to lack of hard substrata.

Sensitivity assessment. This biotope is considered to have a resistance of '**None**' to this pressure. Resilience is '**Very low**' as the pressure represents a permanent change so that sensitivity is assessed as '**High**'.

Physical change (to another sediment type)

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

'Not relevant' on hard bedrock habitats.

Habitat structure changes - removal of substratum (extraction)

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

The species characterizing this biotope occur on rock and would be sensitive to the removal of the habitat. However, extraction of rock substratum is considered unlikely and this pressure is considered to be 'Not relevant' to hard substratum habitats.

Abrasion/disturbance of the surface of the substratum or seabed

Low

Q: Low A: NR C: NR

High

Q: High A: High C: High

Low

Q: Low A: Low C: Low

No direct evidence was found for this pressure on this biotope. Low-level disturbances (e.g. solitary anchors) are unlikely to cause harm to the biotope as a whole, due to the impact's small footprint. Natural abrasion of the lamina tips occurs continuously, even in calm conditions (Krumhansl, 2012) as a result of water friction, although this erosion may be beneficial to the plants, reducing drag on the thalli (Reed *et al.*, 2008, Krumhansl & Scheibling, 2011; Gunnill, 1985). While *Saccharina latissima* is usually permanently attached to the substratum, Burrows (1958) suggests that re-attachment to the substratum after dislodgement is possible with individuals regrowing hapteron branches. It is, therefore, possible that individuals may be able to withstand dislodgement and abrasion. Survival of *Saccharina latissima* in areas where high levels of abrasion occur (a glacial influenced shore) indicate the phenotypic plasticity of the species and suggest that this species, and therefore the habitat, may be resistant to a higher degree of abrasion than other kelp biotopes (Spurkland & Iken, 2011a). Additionally, *Saccharina latissima* was the only kelp species present on an exposed glacial shore, where high levels of abrasion, inorganic sediment and siltation occurred, while an adjacent sheltered site boasted five kelp species (Spurkland & Iken, 2011b).

In a review of the effects of trampling on intertidal habitats, Tyler-Walters & Arnold (2008) found no information on the effects of trampling on *Laminaria* species (*Laminaria digitata* and *Laminaria saccharina*). The authors suggested that laminarians are robust species but that trampling on blades at low tide could potentially damage the blade or growing meristem. Trampling on shallow algal communities in the Mediterranean reported that erect canopy forming species (e.g. *Cysterseira* spp., *Dictyota* spp.) were the worse affected, and suffered a reduction in abundance but were reduced to just holdfasts at high trampling intensities (Milazzo *et al.*, 2002; Tyler-Walters, 2005). *Echinus esculentus* suffer from abrasion via impact from scallop dredges (Bradshaw *et al.*, 2000; Hall-Spencer & Moore, 2000a). While adults may be able to repair some of their test, most impacts result in the death of the organism. Physical abrasion in this biotope is, therefore, likely to decrease grazing on the kelps and may change the identity of the biotope.

Sensitivity assessment. There is little evidence of sensitivity to abrasion in this biotope. Abrasion via trampling could damage parts of the adult kelp and red algae and lead to the removal of individuals. Abrasion by passing bottom trawls or similar gear may remove or damage large erect kelps, and the associated biological assemblage could also be damaged, dislodged or killed.

Therefore, a resistance of '**Low**' is suggested based on limited evidence. Nevertheless, the community is dominated by robust or rapid colonizing species so that resilience is probably '**High**' and hence sensitivity '**Low**'.

Penetration or disturbance of the substratum subsurface

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

The species characterizing this biotope group are epifauna or epiflora occurring on hard rock, which is resistant to subsurface penetration. Therefore, 'penetration' is '**Not relevant**'. The assessment for abrasion at the surface only is, therefore, considered to equally represent sensitivity to this pressure'. Please refer to 'abrasion' above.

Changes in suspended solids (water clarity)

Low

Q: High A: Low C: Medium

High

Q: High A: High C: High

Low

Q: High A: Low C: Medium

Next to wave exposure, light was a key descriptor of *Saccharina latissima*'s distribution along the Norwegian coast, indicating its importance to this biotope's identity (Bekkby & Moy, 2011). This biotope typically occurs in silty conditions, with *Saccharina latissima* able to maintain a positive carbon budget in very low light conditions (Andersen *et al.*, 2011). As a photosynthetic organism, ultimately *Saccharina latissima*'s depth distribution is reliant on light availability (Lüning, 1979; Lüning & Dring, 1979; Gerard, 1988). Therefore an increase in turbidity may lead to the mortality of algae at the biotope's deeper range limit and may limit the biotope to shallower waters.

Blue light is crucial for the gametophytic stages of *Saccharina latissima*, and several other congeneric species (Lüning, 1980). Without blue light (1-4 nE cm/s) and in the presence of red light, female gametophytes do not become fertile or produce eggs (Lüning & Dring, 1975). In comparison to *Laminaria digitata* and *Laminaria hyperborea*, *Saccharina latissima* exhibits a higher level of tolerance to UV light (indicative of its opportunistic nature, Lüning, 1980). Dissolved organic materials (yellow substance or gelbstoff) absorbs blue light (Kirk, 1976), therefore changes in riverine input or other land-based runoff are likely to influence kelp density and distribution. Populations of *Saccharina latissima*'s exhibit different rates of carbon assimilation and growth when exposed to different light acclimation levels in laboratory conditions with alga from turbid sites possessing the fastest growth across treatments (Gerard, 1988). Deep water populations also exhibit adapted characteristics, with daily irradiances exceeding an average of 20 E (radiant flux) /m² /day reduce growth rates. The tolerance of a particular population to this pressure must, therefore, be considered in isolation.

Decreases in suspended solids are initially likely to increase photosynthesis and productivity of *Saccharina latissima*. However, in conditions of greater water clarity (reduced suspended solids), *Laminaria digitata* typically out-competes *Saccharina latissima*, resulting in the loss of the biotope (Norton, 1978). An absence of this biotope in low silt environments is therefore expected, although, with greater water clarity, it may be able to shift its range to deeper waters.

Increases in the levels of suspended sediment were found to reduce growth rates in *Saccharina latissima* (studied as *Laminaria saccharina*) by 20% (Lyngby & Mortensen, 1996). Suspended Particle Matter (SPM) concentration has a linear relationship with subsurface light attenuation (Kd) (Devlin *et al.*, 2008). *Laminaria* spp. show a decrease of 50% photosynthetic activity when turbidity increases by 0.1/m (light attenuation coefficient = 0.1-0.2/m; Staehr & Wernberg, 2009).

Burrow & Pybus (1971) found that the mean thalli thickness of *Saccharina latissima* (studied as *Laminaria saccharina*) that had grown in the silted waters of Redcar, Souter Point and Robin Hood's Bay (North-East England) were significantly smaller than those grown in the clearer waters of St Abbs (North-East England) and Port Erin (Isle of Man). Because of the low water movement associated with this biotope, suspended solids are not likely to be removed by water currents or turbulence and subsequent siltation of the biotope is, therefore, likely. Decreases in siltation may also cause a shift in the identity of the associated assemblage, as suspension and deposit feeders receive fewer nutrients, due to the lower carbon input and suspension feeders benefit as their feeding apparatus suffer less from clogging by silt.

Echinus esculentus has been recorded in suspended material up to 5-6 mg/l (Comely & Ansell, 1988). Ingestion of sediment by this species has been documented, possibly to extract microalgae (Comely & Ansell, 1988). It is unknown to what extent changes to the turbidity at the benchmark level will affect *Echinus esculentus*. The ability of this species to move away from unfavourable conditions suggests that a decrease in grazing could result from a change in turbidity from intermediate to medium turbidity. Red algae are shade tolerant so less sensitive to a reduction in light than the kelp species, although the increased siltation and scour may be detrimental to the less robust species. However, the biotope is dominated by silt and scour tolerant and/or rapid colonizing species.

Sensitivity assessment. A decrease in suspended particulates from e.g. intermediate to clear (see benchmark) is likely to reduce siltation and scour, and allow other kelp species (e.g. *Laminaria digitata*) to increase in abundance with a resultant change in the character of the biotope. The biotope is likely to be replaced by mixed kelp biotopes, depending on the extent of the change in suspended solids and the presence of mobile coarse sediments. An increase in turbidity at the benchmark e.g. from clear to intermediate represents a change from 0.67 to 6.7 in light attenuation coefficient (extracted from Devlin *et al.*, 2008), and a change from intermediate to turbid conditions is considerably greater. Based on the observation that *Laminaria* spp. show a 50% decrease in photosynthetic activity after a change in light attenuation of only 0.1/m it is likely that the growth of *Saccharina latissima* would be significantly decreased. Therefore, the deeper IR.LIR.K.Slat.Pk may be lost, and the depth range of IR.LIR.K.Slat.Ft significantly reduced, and/or replaced by IR.LIR.K.Slat.Pk. Resistance to decreased and increased turbidity is therefore considered to be 'Low'. Resilience is probably 'High'. The biotope, therefore, has 'Low' sensitivity to the pressure.

Smothering and siltation rate changes (light)

High

Q: Low A: NR C: NR

High

Q: High A: High C: High

Not sensitive

Q: Low A: Low C: Low

Low levels of siltation have been shown to initially offer protection to *Saccharina latissima* from UVR in laboratory experiments with thallus samples (Roleda *et al.*, 2008). However, after burial under a variety of sediment types, for over 7 days, symptoms of degradation, bleaching, tissue loss and reduced PSII function, were evident (Roleda & Dethleff, 2011). Laboratory experiments show that even a very thin deposit of fine grained sediment (0.1-0.2 cm thick) caused rotting of *Saccharina latissima*, resulting in 25% mortality if covered for 4 weeks, under conditions of no water movement (Lyngby & Mortensen 1996). In the field, these conditions (no water movement) rarely exist and might explain the survival of *Saccharina latissima* sporophytes in areas of siltation (Birkett *et al.*, 1998b).

The gametophytic and zoospore stages are more vulnerable than their adult counterpart.

Laboratory experiments indicated the adverse effects of siltation on *Saccharina latissima*, including abnormal development of the zoospore (Burrows, 1971). Other studies have indicated that siltation inhibits spore settlement with spores failing to form attachments to the fine sediment or the hard bedrock beneath, resulting in their subsequent loss from the biotope by water activity (Devinny & Volse, 1978, Norton, 1978; Bartsch *et al.*, 2008).

Smothering of the whole sporophytes is unlikely to last for long, if deposition is light (<5 cm) silt is likely to fall from the fronds to the substratum, especially in conditions of weak water movement, therefore the rates of photosynthesis and growth are likely to return to normal within a few days of the deposition event. Also, this is a naturally silty biotope, the organisms should be resistant to this pressure. Epifauna (e.g. ascidians) were reported from vertical surfaces within the biotope, and so are less likely to be smothered (Conner *et al.*, 2004), while the community is depauperate relative to other kelp biotopes because of the siltation and scour.

Sensitivity assessment. Where smothering is short-term (less than 7 days), then this biotope should be relatively resistant. As this biotope is recorded from low energy habitats (wave sheltered and weak tidal streams) deposited sediment may remain for some time, depending on the local conditions and topography. However, as the biotope is typical of silted conditions it is probably resistant of short-term deposition of 5 cm sediment. Therefore, a resistance of 'High' is suggested, although long-term smothering would be detrimental. The resilience of the biotope is considered to be 'High' and the sensitivity of this biotope is, therefore 'Not sensitive' at the benchmark, although confidence is low and local hydrography may increase or decrease the resistance.

Smothering and siltation rate changes (heavy)

Low

Q: Low A: NR C: NR

High

Q: High A: High C: High

Low

Q: Low A: Low C: Low

Low levels of siltation have been shown to initially offer protection to *Saccharina latissima* from UVR in laboratory experiments with thallus samples (Roleda *et al.*, 2008). However, after burial under a variety of sediment types, for over 7 days, symptoms of degradation, bleaching, tissue loss and reduced PSII function, were evident (Roleda & Dethleff, 2011). Laboratory experiments show that even a very thin deposit of fine grained sediment (0.1-0.2 cm thick) caused rotting of *Saccharina latissima*, resulting in 25% mortality if covered for 4 weeks, under conditions of no water movement (Lyngby & Mortensen 1996). In the field, these conditions (no water movement) rarely exist and might explain the survival of *Saccharina latissima* sporophytes in areas of siltation (Birkett *et al.*, 1998b).

The gametophytic and zoospore stages are more vulnerable than their adult counterpart. Laboratory experiments indicated the adverse effects of siltation on *Saccharina latissima*, including abnormal development of the zoospore (Burrows, 1971). Other studies have indicated that siltation inhibits spore settlement with spores failing to form attachments to the fine sediment or the hard bedrock beneath, resulting in their subsequent loss from the biotope by water activity (Devinny & Volse, 1978, Norton, 1978; Bartsch *et al.*, 2008).

Smothering of the whole sporophytes is unlikely to last for long, if deposition is light (<5 cm) silt is likely to fall from the fronds to the substratum, especially in conditions of weak water movement, therefore the rates of photosynthesis and growth are likely to return to normal within a few days of the deposition event. Also, this is a naturally silty biotope, the organisms should be resistant to this pressure. Epifauna (e.g. ascidians) were reported from vertical surfaces within the biotope, and so are less likely to be smothered (Conner *et al.*, 2004), while the community is depauperate relative

to other kelp biotopes because of the siltation and scour.

Sensitivity assessment. Where smothering is short-term (less than 7 days), then this biotope should be relatively resistant. The majority of studies have been done in the laboratory; as a result, their results may not be wholly relevant to the reaction of *Saccharina latissima* to the pressure. As this biotope is recorded from low energy habitats (wave sheltered and weak tidal streams) a deposit of 30 cm of sediment may remain for some time, depending on the local conditions and topography. Such 'Heavy' smothering would probably cover most of the epiflora and epifauna in the biotope (except some on vertical surfaces) and would probably result in death or a significant proportion of the resident species populations, including *Saccharina latissima*. Therefore, the resistance is probably '**Low**'. However, as the resilience is probably '**High**', sensitivity is '**Low**', although confidence is low and local hydrography may increase or decrease the resistance.

Litter

Not Assessed (NA)

Q: NR A: NR C: NR

Not assessed (NA)

Q: NR A: NR C: NR

Not assessed (NA)

Q: NR A: NR C: NR

Not assessed. It is feasible that discarded fishing line, plastic netting, or similar discards could tangle on kelp fronds and potentially damage or remove individuals. However, no documented evidence was found.

Electromagnetic changes

No evidence (NEv)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

No evidence (NEv)

Q: NR A: NR C: NR

No evidence

Underwater noise changes

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant

Introduction of light or shading

Low

Q: Low A: NR C: NR

Very Low

Q: Low A: NR C: NR

High

Q: Low A: Low C: Low

Next to wave exposure, light was a key descriptor of *Saccharina latissima*'s distribution along the Norwegian coast, indicating its importance to this biotope's identity (Bekkby & Moy, 2011). This biotope typically occurs in silty conditions, with *Saccharina latissima* able to maintain a positive carbon budget in very low light conditions (Andersen *et al.*, 2011). As a photosynthetic organism, ultimately *Saccharina latissima*'s depth distribution is reliant on light availability (Lüning, 1979; Lüning & Dring, 1979; Gerard, 1988). Therefore an increase in turbidity may lead to the mortality of algae at the biotope's deeper range limit and may limit the biotope to shallower waters.

Blue light is crucial for the gametophytic stages of *Saccharina latissima*, and several other congeneric species (Lüning, 1980). Without blue light (1-4 nE cm/s) and in the presence of red light, female gametophytes do not become fertile or produce eggs (Lüning & Dring, 1975). In comparison to *Laminaria digitata* and *Laminaria hyperborea*, *Saccharina latissima* exhibits a higher level of tolerance to UV light (indicative of its opportunistic nature, Lüning, 1980). Dissolved organic materials (yellow substance or gelbstoff) absorbs blue light (Kirk, 1976), therefore changes in riverine input or other land-based runoff are likely to influence kelp density and distribution. Populations of

Saccharina latissima's exhibit different rates of carbon assimilation and growth when exposed to different light acclimation levels in laboratory conditions with alga from turbid sites possessing the fastest growth across treatments (Gerard, 1988). Deep water populations also exhibit adapted characteristics, with daily irradiances exceeding an average of 20 E (radiant flux) /m² /day reduce growth rates. The tolerance of a particular population to this pressure must, therefore, be considered in isolation.

Increases in the levels of suspended sediment were found to reduce growth rates in *Saccharina latissima* (studied as *Laminaria saccharina*) by 20% (Lyngby & Mortensen, 1996). Suspended Particle Matter (SPM) concentration has a linear relationship with subsurface light attenuation (Kd) (Devlin *et al.*, 2008). *Laminaria* spp. show a decrease of 50% photosynthetic activity when turbidity increases by 0.1/m (light attenuation coefficient = 0.1-0.2/m; Staehr & Wernberg, 2009). Therefore any activity that decreases incident light (e.g. shading) may be detrimental.

Sensitivity assessment. An increase in incident light is likely to increase plant productivity, and increase the density of *Saccharina latissima* so that the IR.LIR.K.Slat.Ft and IR.LIR.K.Slat.Pk may extend to greater depths. However, there is no evidence that artificial light sources have caused an increase in macroalgal productivity. Constant artificial light may affect the reproductive cues, development of gametophytes etc, but no evidence was found. However, shading, especially from permanent structures (e.g pontoons, jetties) are likely to reduce incident light, and will probably result in the reduction in kelp density, or even its exclusion from the affected area. Therefore, a resistance of '**Low**' is suggested. Resilience is probably 'High' if the shading is temporary but '**Very low**' if permanent. Therefore, a precautionary sensitivity of '**High**' is suggested.

Barrier to species movement

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant – this pressure is considered applicable to mobile species, e.g. fish and marine mammals rather than seabed habitats. Barriers to propagule (larvae, zoospores) supply could adversely affect the population because it is dependent on rapid recolonization after disturbance. However, most of the community, including the kelps, are widespread and also may be self-recruiting within the habitat or between adjacent habitats. Any permanent structures that completely block water exchange would be detrimental but mainly due to the permanent change in hydrography.

Death or injury by collision

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Injury or mortality from collisions of biota with both static and/or moving structures are most relevant to mobile species. Intertidal habitat may be damaged due to the grounding of vessels (boats, ships, tankers etc), and is addressed under 'abrasion' above.

Visual disturbance

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant (NR)

Q: NR A: NR C: NR

Not relevant

Biological Pressures

	Resistance	Resilience	Sensitivity
Genetic modification & translocation of indigenous species	No evidence (NEv) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR

No evidence regarding the genetic modification of the key characterizing species was found. Cultivation of this species is becoming more common and may be achieved in coastal waters far from shore, increasing the species' potential larval dispersal range. There is a high degree of plasticity within this species, as indicated by Gerard (1988), suggesting that this species would be resistant to the introduction of genetically modified populations. No evidence that *Saccharina latissima* cross-breeds with any of its congeneric species was found. Cultivation of this species from translocated individuals does occur, however, the effects of this process on the natural populations of this species are not known (Peteiro *et al.*, 2014).

Sensitivity assessment. No direct evidence was found that might indicate the effects of this pressure on the biotope.

Introduction or spread of invasive non-indigenous species	Medium Q: High A: Medium C: Medium	Low Q: High A: High C: High	Medium Q: High A: Medium C: Medium
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The effects of invasive species on *Saccharina latissima* appear to be limited, or not fully documented in the literature. Strong & Dring (2011) found that the invasive macroalgae, *Sargassum muticum*, did not pose a threat to *Saccharina latissima* stands in Strangford Lough, Northern Ireland, indicating the ability of this species to withstand competition from the invader. However, the grazer, *Lacuna vincta* preferentially grazes on *Saccharina latissima* over the invasive macroalgae *Codium fragile* in the Gulf of Maine, USA (Chavanich & Harris, 2004). If similar conditions exist in UK waters, where native grazers preferentially feed on the native *Saccharina latissima*, then the invasive species will have an initial advantage, and may potentially out-compete *Saccharina latissima*, leading to the loss of the biotope.

The survival of *Saccharina latissima* in harbours and docks despite heavy fouling by epibionts has been documented in the south west of England (Johnston *et al.*, 2011). While the health of this kelp was undetermined; their presence illustrated the resilience of this biotope against this pressure. However, if *Saccharina latissima* is out-competed by invasive macroalgae, its recolonization could be prevented by heavy fouling of non-native origin, in a similar way that native fouling organisms have prevented recolonization and recovery of *Saccharina latissima* beds in the Skagerrak area (Andersen *et al.*, 2011). If an invasion of ephemeral turf algae is coupled with a large-scale disturbance event (e.g. a storm) *Saccharina latissima* is likely to be vulnerable, and consequently, the whole biotope could be at risk (O'Brien *et al.*, 2015).

Sensitivity assessment. Resistance to this pressure is dependent on the identity of the invasive species, thus resistance is recorded as '**Medium**'. Non-indigenous, invasive macroalgae have been shown to prevent native spores from settling and developing, therefore, resilience to this pressure is classed as '**Low**'. Therefore, sensitivity is recorded as '**Medium**'.

Introduction of microbial pathogens**High**
Q: Low A: NR C: NR**High**
Q: High A: High C: High**Not sensitive**
Q: Low A: Low C: Low

Little direct evidence was found in the literature with only two studies found on microscopic algal pathogens. *Saccharina latissima* (studied as *Laminaria saccharina*) may be infected by the microscopic brown alga *Streblonema aecidioides* which may manifest to different degrees from dark spots to heavy deformations and crippled thalli and reduce growth rates. Infection rates have been recorded as 87% ($\pm 13\%$) in Kiel Bay, Western Baltic (Peters & Scaffelke, 1996). Association of *Saccharina latissima* with a marine bacterium, *Pseudomonads* in the Baltic Sea protects the algae from two algal pathogens, *Pseudoalteromonas elyakovii* and *Algicola bacteriolytica*. *Pseudomonads* produce antibiotics which prevent *Saccharina latissima*'s infection, suggesting that this biotope's resistance to disease is population and location specific (Nagel *et al.*, 2012).

However, there is no evidence in the literature that infection by microbial pathogens results in the mass death of kelp populations and the kelp themselves are known to regulate bacterial infections through iodine metabolism (Cosse *et al.*, 2009). Based on the lack of reported mortalities of the characterizing and associated species, the resistance is assessed as '**High**' resistance to this pressure. Hence, resilience is assessed as '**High**' and the biotope is assessed as '**Not sensitive**'.

Removal of target species**None**
Q: High A: Medium C: Medium**High**
Q: High A: High C: High**Medium**
Q: High A: Medium C: Medium

In the UK, harvesting of *Saccharina latissima* is confined to manual harvesting on a small scale and farming. Manual harvesting may involve individual blade or whole alga removal. Only two seaweed leases exist in the UK illustrating the low impact of this species' harvesting in the wild in UK waters. Mechanical harvesting of *Saccharina latissima* is done in Italy, but the preferred method of commercial harvesting in Europe is by farming on ropes (Seaweed Industry in Europe, Netalgae, 2012). Low-level removal of individuals from the shoreline is unlikely to have an effect on the local biotope. However, if harvesting of wild *Saccharina latissima* increased, the time window for harvesting (low tide) is relatively small and could act as a buffer against the excessive harvesting of the species. However, if gathering by diving also increased there would be little resistance to the pressure. Associated species are unlikely to be affected by the low level removal of *Saccharina latissima* unless protection from desiccation on the lower shore is important.

Overfishing of apex predators (in particular fin fish), has been occurring for centuries in the UK and Irish waters, resulting in habitats dominated by invertebrates and commercially undesirable fish such as the lesser spotted cat shark (Molfese *et al.*, 2014) suggesting an ecosystem level shift in the functioning of these food webs. The urchin barrens recorded off the coast of Norway and in the North West Atlantic, are not common to UK waters. The deforestation by urchins is restricted and patchy (although some have been noted in Scotland; Smale *et al.*, 2013) but could be a result of this shift, leading to a temporally more stable, less dynamic biotope.

Sensitivity assessment. Due to the methods of harvesting used for *Saccharina latissima*, with the emphasis on aquaculture rather than wild harvesting, little evidence for the resilience of this biotope to harvesting exists. It can be presumed however that if harvesting of the species occurred extensively in an area then there would be little resistance to the pressure. Resistance is regarded as '**None**' as the pressure is defined as the removal of key characterizing species from the biotope.

Nevertheless, resilience is probably '**High**', so that sensitivity to this pressure is defined as '**Medium**'.

Removal of non-target species

Low

Q: Low A: High C: High

Medium

Q: High A: High C: High

Medium

Q: Medium A: High C: High

No direct evidence was found for the removal of *Saccharina latissima* (or *Laminaria digitata*) from a biotope as by-catch. However, if they were removed as by-catch, the result would be the loss of the biotope. In healthy macroalgae communities, many species contribute to the balanced condition of the ecosystem. Disrupting this balance may cause top-down consequences for the biotope; for example, overfishing of top predators in Norwegian waters was thought to have resulted in an urchin bloom, subsequent overgrazing and proliferation of urchin barrens (Steneck *et al.*, 2004).

Sensitivity assessment. Resistance to this pressure is considered '**Low**' as removal of a proportion of the structuring species would significantly alter the character of the biotope. Therefore, resilience is assessed as '**High**' and sensitivity as '**Low**'.

Bibliography

- Andersen, G.S., 2013. Patterns of *Saccharina latissima* recruitment. *Plos One*, **8** (12), e81092.
- Andersen, G.S., Pedersen, M.F. & Nielsen, S.L., 2013. Temperature, Acclimation and Heat Tolerance of photosynthesis in Norwegian *Saccharina latissima* (Laminariales, Phaeophyceae). *Journal of Phycology*, **49** (4), 689-700.
- Andersen, G.S., Steen, H., Christie, H., Fredriksen, S. & Moy, F.E., 2011. Seasonal patterns of sporophyte growth, fertility, fouling, and mortality of *Saccharina latissima* in Skagerrak, Norway: implications for forest recovery. *Journal of Marine Biology*, **2011**, Article ID 690375, 8 pages.
- Bartsch, I., Vogt, J., Pehlke, C. & Hanelt, D., 2013. Prevailing sea surface temperatures inhibit summer reproduction of the kelp *Laminaria digitata* at Helgoland (North Sea). *Journal of Phycology*, **49** (6), 1061-1073.
- Bartsch, I., Wiencke, C., Bischof, K., Buchholz, C.M., Buck, B.H., Eggert, A., Feuerpfeil, P., Hanelt, D., Jacobsen, S. & Karez, R., 2008. The genus *Laminaria* sensu lato: recent insights and developments. *European Journal of Phycology*, **43** (1), 1-86.
- Bekkby, T. & Moy, F.E., 2011. Developing spatial models of sugar kelp (*Saccharina latissima*) potential distribution under natural conditions and areas of its disappearance in Skagerrak. *Estuarine Coastal and Shelf Science*, **95** (4), 477-483.
- Bernstein, B.B., Williams, B.E. & Mann, K.H., 1981. The role of behavioral responses to predators in modifying urchins' (*Strongylocentrotus droebachiensis*) destructive grazing and seasonal foraging patterns. *Marine Biology*, **63** (1), 39-49.
- Bishop, G.M., 1985. *Aspects of the reproductive ecology of the sea urchin Echinus esculentus* L. Ph.D. thesis, University of Exeter, UK.
- Bolton, J.J. & Lüning, K.A.F., 1982. Optimal growth and maximal survival temperatures of Atlantic *Laminaria* species (Phaeophyta) in culture. *Marine Biology*, **66**, 89-94.
- Bonsdorff, E. & Vahl, O., 1982. Food preferences of the sea urchins *Echinus actus* and *Echinus esculentus*. *Marine Behaviour and Physiology*, **8** (3), 243-248.
- Booolootian, R.A., 1966. *Physiology of Echinodermata*. (Ed. R.A. Booolootian), pp. 822-822. New York: John Wiley & Sons.
- Borum, J., Pedersen, M.F., Krause-Jensen, D., Christensen, P.B. & Nielsen, K., 2002. Biomass, photosynthesis and growth of *Laminaria saccharina* in a high-arctic fjord, NE Greenland. *Marine Biology*, **141**, 11-19.
- Bradshaw, C., Veale, L.O., Hill, A.S. & Brand, A.R., 2000. The effects of scallop dredging on gravelly seabed communities. In: *Effects of fishing on non-target species and habitats* (ed. M.J. Kaiser & de S.J. Groot), pp. 83-104. Oxford: Blackwell Science.
- Buck, B.H. & Buchholz, C.M., 2005. Response of offshore cultivated *Laminaria saccharina* to hydrodynamic forcing in the North Sea. *Aquaculture*, **250** (3-4), 674-691.
- Burrows, E.M. & Pybus, C., 1971. *Laminaria saccharina* and marine pollution in North-East England. *Marine Pollution Bulletin*, **2**, 53-56.
- Burrows, E.M., 1958. Sublittoral algal population in Port Erin Bay, Isle of Man. *Journal of the Marine Biological Association of the United Kingdom*, **37**, 687-703.
- Burrows, E.M., 1971. Assessment of pollution effects by the use of algae. *Proceedings of the Royal Society of London, Series B*, **177**, 295-306.
- Chapman, A.R.O., 1981. Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St. Margaret's Bay, Eastern Canada. *Marine Biology*, **62**, 307-311.
- Chavanich, S. & Harris, L.G., 2004. Impact of the non-native macroalga *Codium fragile* (sur.) *hariot* ssp. *tomentosoides* (van goor) *silva* on the native snail *Lacuna vincta* (montagu, 1803) in the gulf of maine. *Veliger*, **47** (2), 85-90.
- Cie, D.K. & Edwards, M.S., 2011. Vertical distribution of kelp zoospores. *Phycologia*, **50** (4), 340-350.
- Cole, S., Codling, I.D., Parr, W., Zabel, T., 1999. Guidelines for managing water quality impacts within UK European marine sites [On-line]. *UK Marine SACs Project*. [Cited 26/01/16]. Available from: http://www.ukmarinesac.org.uk/pdfs/water_quality.pdf
- Comely, C.A. & Ansell, A.D., 1988. Invertebrate associates of the sea urchin, *Echinus esculentus* L., from the Scottish west coast. *Ophelia*, **28**, 111-137.
- Conolly N.J. & Drew, E.A., 1985. Physiology of *Laminaria*. III. Effect of a coastal eutrophication on seasonal patterns of growth and tissue composition in *Laminaria digitata* and *L. saccharina*. *Marine Ecology, Pubblicazioni della Stazione Zoologica di Napoli I*, **6**, 181-195.
- Cosse, A., Potin, P. & Leblanc, C., 2009. Patterns of gene expression induced by oligoguluronates reveal conserved and environment-specific molecular defence responses in the brown alga *Laminaria digitata*. *New Phytologist*, **182** (1), 239-250.
- Davison, I.R., Greene, R.M. & Podolak, E.J., 1991. Temperature acclimation of respiration and photosynthesis in the brown alga *Laminaria saccharina*. *Marine Biology*, **110**, 449-454.
- Dayton, P.K. & Tegner, M.J., 1984. Catastrophic storms, El-Nino, and patch stability in a southern-california kelp community. *Science*, **224** (4646), 283-285.
- Devinny, J. & Volse, L., 1978. Effects of sediments on the development of *Macrocystis pyrifera* gametophytes. *Marine Biology*, **48** (4), 343-348.
- Devlin, M.J., Barry, J., Mills, D.K., Gowen, R.J., Foden, J., Sivyver, D. & Tett, P., 2008. Relationships between suspended particulate material, light attenuation and Secchi depth in UK marine waters. *Estuarine, Coastal and Shelf Science*, **79** (3), 429-439.

- Druehl, L.D., 1967. Distribution of two species of *Laminaria* as related to some environmental factors 1. *Journal of Phycology*, **3**(2), 103-108.
- Druehl, L.D., 1970. The pattern of Laminariales distribution in the northeast Pacific. *Phycologia*, **9** (3), 237-247.
- Estes, J.A. & Duggins, D.O., 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecological Monographs*, **65**, 75-100.
- Frieder, C., Nam, S., Martz, T. & Levin, L., 2012. High temporal and spatial variability of dissolved oxygen and pH in a nearshore California kelp forest. *Biogeosciences*, **9** (10), 3917-3930.
- Gaylord, B., Reed, D.C., Raimondi, P.T. & Washburn, L., 2006. Macroalgal spore dispersal in coastal environments: Mechanistic insights revealed by theory and experiment. *Ecological Monographs*, **76** (4), 481-502.
- Gayral, P. & Cosson, J., 1973. Exposé synoptique des données biologiques sur la laminaire digitée *Laminaria digitata*. *Synopsis FAO sur les pêches*, no. **89**.
- Gerard, V., 1982. In situ water motion and nutrient uptake by the giant kelp *Macrocystis pyrifera*. *Marine Biology*, **69** (1), 51-54.
- Gerard, V.A. & Du Bois, K.R., 1988. Temperature ecotypes near the southern boundary of the kelp *Laminaria saccharina*. *Marine Biology*, **97**, 575-580.
- Gerard, V.A., 1987. Hydrodynamic streamlining of *Laminaria saccharina* Lamour. in response to mechanical stress. *Journal of Experimental Marine Biology and Ecology*, **107**, 237-244.
- Gerard, V.A., 1988. Ecotypic differentiation in light-related traits of the kelp *Laminaria saccharina*. *Marine Biology*, **97**, 25-36.
- Gessner, F., 1970. Temperature - Plants. In *Marine Ecology: A Comprehensive Treatise on Life in Oceans and Coastal Waters*. Vol. 1 *Environmental Factors Part 1*. (ed. O. Kinne), pp. 363-406. Chichester: John Wiley & Sons
- Gorgula, S.K. & Connell, S.D., 2004. Expansive covers of turf-forming algae on human-dominated coast: the relative effects of increasing nutrient and sediment loads. *Marine Biology*, **145** (3), 613-619.
- Griffiths, A.B., Dennis, R. & Potts, G.W., 1979. Mortality associated with a phytoplankton bloom off Penzance in Mount's Bay. *Journal of the Marine Biological Association of the United Kingdom*, **59**, 515-528.
- Gunnill, F., 1985 Population fluctuations of seven macroalgae in southern California during 1981-1983 including effects of severe storms and an El Nino. *Journal of Experimental Marine Biology and Ecology*, **85**, 149-164.
- Hall-Spencer, J.M. & Moore, P.G., 2000a. Impact of scallop dredging on maerl grounds. In *Effects of fishing on non-target species and habitats*. (ed. M.J. Kaiser & S.J., de Groot) 105-117. Oxford: Blackwell Science.
- Harder, D.L., Hurd, C.L. & Speck, T., 2006. Comparison of mechanical properties of four large, wave-exposed seaweeds. *American Journal of Botany*, **93** (10), 1426-1432.
- Heinrich, S., Valentin, K., Frickenhaus, S., John, U. & Wiencke, C., 2012. Transcriptomic analysis of acclimation to temperature and light stress in *Saccharina latissima* (Phaeophyceae). *Plos One*, **7** (8), e44342.
- Hiscock, K. & Hoare, R., 1975. The ecology of sublittoral communities at Abereiddy Quarry, Pembrokeshire. *Journal of the Marine Biological Association of the United Kingdom*, **55**, 833-864.
- Hurd, C.L., 2000. Water motion, marine macroalgal physiology, and production. *Journal of Phycology*, **36** (3), 453-472.
- Isaeus, M., 2004. Factors structuring *Fucus communities* at open and complex coastlines in the Baltic Sea. Department of Botany, Botaniska institutionen, Stockholm.
- Jensen, A.C., Collins, K.J., Lockwood, A.P.M., Mallinson, J.J. & Turnpenny, W.H., 1994. Colonization and fishery potential of a coal-ash artificial reef, Poole Bay, United Kingdom. *Bulletin of Marine Science*, **55**, 1263-1276.
- JNCC, 2015. The Marine Habitat Classification for Britain and Ireland Version 15.03. (20/05/2015). Available from <https://mhc.jncc.gov.uk/>
- JNCC, 2015. The Marine Habitat Classification for Britain and Ireland Version 15.03. (20/05/2015). Available from <https://mhc.jncc.gov.uk/>
- Johnston, E., Marzinelli, E., Wood, C., Speranza, D. & Bishop, J., 2011. Bearing the burden of boat harbours: Heavy contaminant and fouling loads in a native habitat-forming alga. *Marine Pollution Bulletin*, **62** (10), 2137-2144.
- Kain, J.M., 1975a. Algal recolonization of some cleared subtidal areas. *Journal of Ecology*, **63**, 739-765.
- Kain, J.M., 1979. A view of the genus *Laminaria*. *Oceanography and Marine Biology: an Annual Review*, **17**, 101-161.
- Kain, J.M., 1987. Photoperiod and temperature as triggers in the seasonality of *Delesseria sanguinea*. *Helgolander Meeresuntersuchungen*, **41**, 355-370.
- Karsten, U., 2007. Research note: salinity tolerance of Arctic kelps from Spitsbergen. *Phycological Research*, **55** (4), 257-262.
- Kinne, O., 1977. International Helgoland Symposium "Ecosystem research": summary, conclusions and closing. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, **30**(1-4), 709-727.
- Kirk, J., 1976. Yellow substance (gelbstoff) and its contribution to the attenuation of photosynthetically active radiation in some inland and coastal south-eastern Australian waters. *Marine and Freshwater Research*, **27** (1), 61-71.
- Kirst, G., 1990. Salinity tolerance of eukaryotic marine algae. *Annual review of plant biology*, **41** (1), 21-53.
- Kirst, G.O. & Wiencke, C., 1995. Ecophysiology of polar algae. *Journal of Phycology*, **31** (2), 181-199.

- Krumhansl, K.A. & Scheibling, R.E., 2011. Detrital production in Nova Scotian kelp beds: patterns and processes. *Marine Ecological Progress Series*, **421**, 67-82.
- Krumhansl, K.A. & Scheibling, R.E., 2012. Detrital subsidy from subtidal kelp beds is altered by the invasive green alga *Codium fragile* ssp *fragile*. *Marine Ecology Progress Series*, **456**, 73-85.
- Krumhansl, K.A., 2012. *Detrital production in kelp beds*. degree of Doctor of Philosophy, Department of Biology, Dalhousie University, Halifax, Nova Scotia.
- Lüning, K., 1979. Growth strategy of three *Laminaria* species (Phaeophyceae) inhabiting different depth zones in the sublittoral region of Hegloland (North Sea). *Marine Ecological Progress Series*, **1**, 195-207.
- Lawrence, J.M., 1975. On the relationships between marine plants and sea urchins. *Oceanography and Marine Biology: An Annual Review*, **13**, 213-286.
- Lee, J.A. & Brinkhuis, B.H., 1988. Seasonal light and temperature interaction effects on development of *Laminaria saccharina* (Phaeophyta) gametophytes and juvenile sporophytes. *Journal of Phycology*, **24**, 181-191.
- Levin, P.S., Coyer, J.A., Petrik, R. & Good, T.P., 2002. Community-wide effects of nonindigenous species on temperate rocky reefs. *Ecology*, **83**(11), 3182-3193.
- Ling, S.D., Johnson, C.R., Frusher, S.D. & Ridgeway, K.R., 2009. Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. *Proceedings of the National Academy of Sciences USA*, **106**, 22341-22345.
- Lobban, C.S. & Harrison, P.J. (eds.), 1994. *Seaweed Ecology and Physiology*. Cambridge, uk: Cambridge University Press, pp. 366.
- Lobban, C.S. & Harrison, P.J., 1997. *Seaweed ecology and physiology*. Cambridge: Cambridge University Press.
- Lüning, K., 1990. *Seaweeds: their environment, biogeography, and ecophysiology*: John Wiley & Sons.
- Lüning, K. & Dring, M.J., 1975. Reproduction, growth and photosynthesis of gametophytes of *Laminaria saccharina* grown in blue and red light. *Marine Biology*, **29**, 195-200.
- Lüning, K., 1980. Critical levels of light and temperature regulating the gametogenesis of three laminaria species (Phaeophyceae). *Journal of Phycology*, **16**, 1-15.
- Lyngby, J.E. & Mortensen, S.M., 1996. Effects of dredging activities on growth of *Laminaria saccharina*. *Marine Ecology, Pubblicazioni della Stazione Zoologica di Napoli I*, **17**, 345-354.
- Müller, R., Laepple, T., Bartsch, I. & Wiencke, C., 2009. Impact of oceanic warming on the distribution of seaweeds in polar and cold-temperate waters. *Botanica Marina*, **52** (6), 617-638.
- Milazzo, M., Chemello, R., Badalamenti, F. & Riggio, S., 2002. Short-term effect of human trampling on the upper infralittoral macroalgae of Ustica Island MPA (western Mediterranean, Italy). *Journal of the Marine Biological Association of the UK*, **82** (05), 745-748.
- Molfese, C., Beare, D. & Hall-Spencer, J.M., 2014. Overfishing and the Replacement of Demersal Finfish by Shellfish: An Example from the English Channel. *Plos One*, **9** (7).
- Moy, F., Alve, E., Bogen, J., Christie, H., Green, N., Helland, A., Steen, H., Skarbøvik, E. & Stålnacke, P., 2006. Sugar Kelp Project: Status Report No 1. *SFT Report TA-2193/2006, NIVA Report 5265 (in Norwegian, with English Abstract)*, 36 pp.
- Moy, F.E. & Christie, H., 2012. Large-scale shift from sugar kelp (*Saccharina latissima*) to ephemeral algae along the south and west coast of Norway. *Marine Biology Research*, **8** (4), 309-321.
- Nagel, K., Schneemann, I., Kajahn, I., Labes, A., Wiese, J. & Imhoff, J.F., 2012. Beneficial effects of 2,4-diacetylphloroglucinol-producing pseudomonads on the marine alga *Saccharina latissima*. *Aquatic Microbial Ecology*, **67** (3), 239-249.
- Netalgae, 2012. Seaweed industry in Europe. <http://www.netalgae.eu/publications.php>: (24/04/2014).
- Nielsen, M., Krause-Jensen, D., Olesen, B., Thinggaard, R., Christensen, P. & Bruhn, A., 2014a. Growth dynamics of *Saccharina latissima* (Laminariales, Phaeophyceae) in Aarhus Bay, Denmark, and along the species' distribution range. *Marine Biology*, **161** (9), 2011-2022.
- Nimura, K., Mizuta, H. & Yamamoto, H., 2002. Critical contents of nitrogen and phosphorus for sorus formation in four *Laminaria* species. *Botanica Marina*, **45**, 184-188.
- Norton, T.A., 1978. The factors influencing the distribution of *Saccorhiza polyschides* in the region of Lough Ine. *Journal of the Marine Biological Association of the United Kingdom*, **58**, 527-536.
- Norton, T.A., 1992. Dispersal by macroalgae. *British Phycological Journal*, **27**, 293-301.
- O'Brien, J.M., Scheibling, R.E. & Krumhansl, K.A., 2015. Positive feedback between large-scale disturbance and density-dependent grazing decreases resilience of a kelp bed ecosystem. *Marine Ecology Progress Series*, **522**, 1-13.
- Oates, B.R., 1985. Photosynthesis and amelioration of desiccation in the intertidal saccate alga *Colporema peregrina*. *Marine Biology*, **89**, 109-119.
- Oates, B.R., 1986. Components of photosynthesis in the intertidal saccate alga *Halosaccion americanum* (Rhodophyta, Palmariales). *Journal of Phycology*, **22**, 217-223.
- Parke, M., 1948. Studies on British Laminariaceae. I. Growth in *Laminaria saccharina* (L.) Lamour. *Journal of the Marine Biological Association of the United Kingdom*, **27**, 651-709.
- Parker, H., 1981. Influence of relative water motion on the growth, ammonium uptake and carbon and nitrogen composition of

Ulva lactuca (Chlorophyta). *Marine Biology*, **63** (3), 309-318.

Parker, H., 1982. Effects of simulated current on the growth rate and nitrogen metabolism of *Gracilaria tikvahiae* (Rhodophyta). *Marine Biology*, **69** (2), 137-145.

Pérez, R., 1971. Écologie, croissance et régénération, teneurs en acide alginique de *Laminaria digitata* sur les cotes de la Manche. *Revue des Travaux de l'Institut des Pêches Maritimes*, **35**, 287-346.

Peteiro, C. & Freire, O., 2013. Biomass yield and morphological features of the seaweed *Saccharina latissima* cultivated at two different sites in a coastal bay in the Atlantic coast of Spain. *Journal of Applied Phycology*, **25**(1), 205-213.

Peteiro, C., Sánchez, N., Dueñas-Liaño, C. & Martínez, B., 2014. Open-sea cultivation by transplanting young fronds of the kelp *Saccharina latissima*. *Journal of Applied Phycology*, **26** (1), 519-528.

Peters, A.F. & Schaffelke, B., 1996. *Streblonema* (Ectocarpales, Phaeophyceae) infection in the kelp *Laminaria saccharina* in the western Baltic. *Hydrobiologia*, **326/327**, 111-116.

Pihl, L., Wennhage, H. & Nilsson, S., 1994. Fish assemblage structure in relation to macrophytes and filamentous epiphytes in shallow non-tidal rocky-and soft-bottom habitats. *Environmental Biology of Fishes*, **39** (3), 271-288.

Reed, D.C., Rassweiler, A. & Arkema, K.K., 2008. Biomass rather than growth rate determines variation in net primary production by giant kelp. *Ecology and evolution*, **89**, 2493-2505

Rietema, H., 1993. Ecotypic differences between Baltic and North Sea populations of *Delesseria sanguinea* and *Membranoptera alata*. *Botanica Marina*, **36**, 15-21.

Robins, P.E., Neill, S.P., Giménez, L., Jenkins, S.R. & Malham, S.K., 2013. Physical and biological controls on larval dispersal and connectivity in a highly energetic shelf sea. *Limnology and Oceanography*, **58**(2), 505-524.

Roleda, M.Y. & Dethleff, D., 2011. Storm-generated sediment deposition on rocky shores: Simulating burial effects on the physiology and morphology of *Saccharina latissima* sporophytes. *Marine Biology Research*, **7** (3), 213-223.

Russell, M., 2013. Echinoderm Responses to Variation in Salinity. *Advances in Marine Biology*, **66**, 171-212.

Saier, B. & Chapman, A.S., 2004. Crusts of the alien bryozoan *Membranipora membranacea* can negatively impact spore output from native kelps (*Laminaria longicurvis*). *Botanica Marina*, **47** (4), 265-271.

Sanderson, J., Dring, M., Davidson, K. & Kelly, M., 2012. Culture, yield and bioremediation potential of *Palmaria palmata* (Linnaeus) Weber & Mohr and *Saccharina latissima* (Linnaeus) adjacent to fish farm cages in northwest Scotland. *Aquaculture*, **354**, 128-135.

Scheibling, R.E. & Gagnon, P., 2006. Competitive interactions between the invasive green alga *Codium fragile* ssp *tomentosoides* and native canopy-forming seaweeds in Nova Scotia (Canada). *Marine Ecology Progress Series*, **325**, 1-14.

Scheibling, R.E., Hennigar, A.W. & Balch, T., 1999. Destructive grazing, epiphytism, and disease: the dynamics of sea urchin-kelp interactions in Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences*, **56** (12), 2300-2314.

Sebens, K.P., 1985. Community ecology of vertical rock walls in the Gulf of Maine: small-scale processes and alternative community states. In *The Ecology of Rocky Coasts: essays presented to J.R. Lewis, D.Sc.* (ed. P.G. Moore & R. Seed), pp. 346-371. London: Hodder & Stoughton Ltd.

Sebens, K.P., 1986. Spatial relationships among encrusting marine organisms in the New England subtidal zone. *Ecological Monographs*, **56**, 73-96.

Smale, D.A. & Wernberg, T., 2013. Extreme climatic event drives range contraction of a habitat-forming species. *Proceedings of the Royal Society B-Biological Sciences*, **280** (1754).

Smale, D.A., Burrows, M.T., Moore, P., O'Connor, N. & Hawkins, S.J., 2013. Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective. *Ecology and evolution*, **3** (11), 4016-4038.

Spurkland, T. & Iken, K., 2011a. Salinity and irradiance effects on growth and maximum photosynthetic quantum yield in subarctic *Saccharina latissima* (Laminariales, Laminariaceae). *Botanica Marina*, **54**, 355-365.

Spurkland, T. & Iken, K., 2011b. Kelp Bed Dynamics in Estuarine Environments in Subarctic Alaska. *Journal of Coastal Research*, 133-143.

Staehr, P.A. & Wernberg, T., 2009. Physiological responses of *Ecklonia radiata* (Laminariales) to a latitudinal gradient in ocean temperature. *Journal of Phycology*, **45**, 91-99.

Steneck, R.S., Vavrinc, J. & Leland, A.V., 2004. Accelerating trophic-level dysfunction in kelp forest ecosystems of the western North Atlantic. *Ecosystems*, **7** (4), 323-332.

Stickle, W.B. & Diehl, W.J., 1987. Effects of salinity on echinoderms. In *Echinoderm Studies, Vol. 2* (ed. M. Jangoux & J.M. Lawrence), pp. 235-285. A.A. Balkema: Rotterdam.

Strong, J.A. & Dring, M.J., 2011. Macroalgal competition and invasive success: testing competition in mixed canopies of *Sargassum muticum* and *Saccharina latissima*. *Botanica Marina*, **54** (3), 223-229.

Tyler, P.A. & Young, C.M., 1998. Temperature and pressures tolerances in dispersal stages of the genus *Echinus* (Echinodermata: Echinoidea): prerequisites for deep sea invasion and speciation. *Deep Sea Research II*, **45**, 253-277

Tyler-Walters, H., 2005b. Assessment of the potential impacts of coasteering on rocky intertidal habitats in Wales. *Report to Cyngor Cefn Gwlad Cymru / Countryside Council for Wales from the Marine Life Information Network (MarLIN)*. Marine Biological Association of the United Kingdom, Plymouth, 129 pp.

Tyler-Walters, H. & Arnold, C., 2008. Sensitivity of Intertidal Benthic Habitats to Impacts Caused by Access to Fishing Grounds.

- Report to Cyngor Cefn Gwlad Cymru / Countryside Council for Wales from the Marine Life Information Network (MarLIN) [Contract no. FC 73-03-327], Marine Biological Association of the UK, Plymouth, 48 pp. Available from: www.marlin.ac.uk/publications
- Van den Hoek, C. & Donze, M., 1967. Algal phytogeography of the European Atlantic coasts. *Blumea*, **15** (1), 63-89.
- Van den Hoek, C., Mann, D.G. & Jahns, H.M., 1995. *Algae: an introduction to phycology*: Cambridge University Press.
- Wang, X., Broch, O.J., Forbord, S., Handa, A., Skjermo, J., Reitan, K.I., Vadstein, O. & Olsen, Y., 2014. Assimilation of inorganic nutrients from salmon (*Salmo salar*) farming by the macroalgae (*Saccharina latissima*) in an exposed coastal environment: implications for integrated multi-trophic aquaculture. *Journal of Applied Phycology*, **26** (4), 1869-1878.
- Weile, K., 1996. Baseline study of *Laminaria* populations in Øresund. Doc. nr. 95/120/1E. By VRI/Toxicon AB for Øresundskonsortiet
- Wernberg, T., Smale, D.A., Tuya, F., Thomsen, M.S., Langlois, T.J., de Bettignies, T., Bennett, S. & Rousseaux, C.S., 2013. An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change*, **3** (1), 78-82.
- Wheeler, W.N., 1980. Effect of boundary layer transport on the fixation of carbon by the giant kelp *Macrocystis pyrifera*. *Marine Biology*, **56**, 103-110.
- Wilce, R., 1965. Studies in the genus *Laminaria*. III. A revision of the north Atlantic species of the Simplicies section of *Laminaria*. *Bot. gothoburg.*, **3**, 247-256.
- Wolff, W.J., 1968. The Echinodermata of the estuarine region of the rivers Rhine, Meuse and Scheldt, with a list of species occurring in the coastal waters of the Netherlands. *The Netherlands Journal of Sea Research*, **4**, 59-85.
- Yarish, C., Penniman, C.A. & Egan, B., 1990. Growth and reproductive responses of *Laminaria longicruris* (Laminariales, Phaeophyta) to nutrient enrichment. *Hydrobiologia*, **204**, 505-511.